Some observations on the pattern of labyrinth and neck reflexes and their interactions in both normal and hemilabyrinthectomized cats.

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by

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CONTENTS PAGE

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Summary.

Lindsay, Roberts and Rosenberg (1976) using natural stimulation techniques demonstrated asymmetrically oraganized tonic labyrinth and neck reflexes acting on forelimb extensors. Static tilts of the head alone generated labyrinth reflexes, while rotation of the axis vertebra following denervation of C1 and C2 cervical joints generated neck reflexes independently of labyrinth reflexes. Side-down tilts of the head resulted in a shortening of the medial head of triceps, and conversely for side-up head tilts. Following neck rotation the triceps muscle was observed to lengthen with side-up rotations and to shorten during side-down rotations. Studies on the interaction of labyrinth and neck reflexes demonstrated that when labyrinth and neck reflexes were simultaneously generated no net alteration in muscular activity was observed. This result supports several theoretical schemes which require labyrinth and neck reflexes to interact in such a way as to provide effective stabilisation of the trunk during voluntary head movements. Although Lindsay et al. (1976) described labyrinth and neck actions on forelimb extensors, the participation of flexor muscles in these reflexes remained uncertain, and largely circumstantial. In the first part of this thesis the participation of flexor

muscles in the above reflexes was examined.

Labyrinth and neck reflexes were studied by recording EMG activity in forelimb extensors and flexors in decerebrate cats during periods of natural vestibular and/or neck proprioceptor stimulation. The stimulation techniques were as described by Lindsay et al. (1976). Head rotation alone evoked labyrinth reflexes while rotation of the axis vertebra induced neck reflexes. EMG records obtained during labyrinthine and neck stimulation revealed the distinct presense of labyrinth and neck reflexes in forelimb flexors. The extensor pattern of reflexes conformed to the scheme outlined by Lindsay et al. (1976). Labyrinth reflexes recorded from biceps and brachialis were commonly observed to display tonic activity changes that were well correlated with head position. Tonic labyrinth reflexes in flexors were observed to be reciprocal to those recorded simultaneously from antagonist extensor muscles (triceps). Side-down head tilts depressed flexor EMG activity while side-up head tilts facilitated flexor EMG. Neck reflexes onto flexor muscles displayed the opposite pattern of reflexes for the same direction of rotation; i.e., increased flexor EMG accompanied neck side-down tilts, while depression of flexor EMG occurred with neck side-up tilts. Thus a scheme of labyrinth and neck reflexes can be presented that extends the original results of Lindsay et al. (1976) to include the participation of flexor muscles in reflex stabilization of the trunk.

The role of the labyrinths in aspects of postural control can be recognised following unilateral

labyrinthectomy. Hemilabyrinthectomy inflicts severe postural abnormalities on the behaviour of conscious animals, however, given sufficent time, the signs of disruption diminish and a complete compensation for the lesion appears to have taken place. In studies of this process of compensation little is known about the disruption to the tonic labyrinth and neck reflex systems following hemilabyrinthectomy. In this study the pattern of labyrinth and neck reflexes were examined in both acute hemilabyrinthectomized cats, and cats allowed to recover from the lesion. In acute animals it was found that labyrinth reflexes in extensors and flexors ipsilateral to the side of the lesion appeared normal, while labyrinth reflexes contralateral to the lesion were reversed in comparison to normal. Neck reflexes were unaltered by hemilabyrinthectomy. Consequently, labyrinth and neck reflex interactions are altered giving rise to a new pattern of interaction which may account for some of the observed postural abnormalities seen with hemilabyrinthectomy. Furthermore, the observation that the normal labyrinth reflex is dependant on the integrity of the contralateral labyrinth supports electrophysiological evidence that these reflexes are mediated predominantly by crossed pathways.

In chronic cats, allowed a minimum of 8 weeks recovery, the labyrinth and neck reflexes contralateral to the original lesion regain their normal form, while labyrinth and neck reflexes on the side of the lesion, although normal in the extensor are reversed in the flexor

muscles. The flexors and extensors on the side of the original lesion display parallel activity changes during labyrinth and neck reflexes. It therefore appears that in the compensated animal there has been a re-organisation of labyrinth and neck reflexes. The normal pattern has been restored to the limb contralateral to the lesion (which in the acute showed reversed reflexes), but in the limb ipsilateral to the lesion labyrinth and neck reflex expression in flexor muscles has been reversed giving coactivation of flexors and extensors. Despite this the complete pattern of labyrinth and neck reflexes in the compensated animal can still be considered appropriate for providing effective postural stabilisation by regulating the overal stiffness of one limb, and by altering the distribution of tone in the other, as in the normal reciprocal fashion.

In addition to the above studies experiments were performed on both normal and acute decerebrated cats which examined the interaction of labyrinth and neck reflex systems with elbow joint afferents. In these experiments head, neck and elbow position was used to condition both crossed extensor and ipsilateral flexion reflexes. The results indicate that head and neck position modulate reflex excitability in flexors and extensors in a manner consistant with observations on the direction of labyrinth and neck reflexes in these muscles, and that elbow position can effectively modulate these actions independently of changes in muscle length. Extensor reflex excitability was greatest in normal cats when the elbow was flexed and the

head tilted side-down or the neck tilted side-up. Flexor excitability was greatest with the limb held in extension and the head tilted side-up or the neck side-down. In acute animals the labyrinth actions were altered in agreement with the description of labyrinth reflexes in these animals. The ability of joint afferents to modulate descending labyrinth and neck inputs to motoneurones is taken to indicate that limb position can effectively regulate the reflex output of the labyrinth and neck systems so as to generate reflexes that are appropriate for the position of the limb at any particular time.

Introduction.

The past fifteen years has witnessed a renewal of interest in vestibular physiology and has led to the generation of large bodies of literature covering the detailed neuroanatomy of the vestibular system, vestibulospinal reflexes, vestibulo-ocular reflexes and the process of compensation following hemilabyrinthectomy. Despite a greater understanding of the organisation of the vestibular system there still remain certain areas in which progress has been slow. This thesis is concerned with two problem areas.

One such area concerns the participation and behaviour of limb flexors during positional reflexes originating from the otoliths. Consequently, the pattern of reflex interactions with other positional reflexes, notably those originating from proprioceptors located in the cervical region, has yet to be fully described. In addition, information regarding patterns of interactions with proprioceptive reflexes arising from the limbs is lacking.

Labyrinth and neck reflexes are known to influence limb posture. It is not known, however, whether limb position itself can influence these reflexes. A candidate for a proprioceptive system capable of such action are the joint receptors, a population of which are known to possess discharge characteristics related to position. By utilizing natural stimulation techniques it is hoped to study the reflex behaviour of forelimb flexors and their relationship

with activity in extensors during labyrinth and neck reflexes. The effects of altering limb position on the efficacy of labyrinth and neck reflexes will also be assessed. It is hoped therefore to describe a scheme of interactive influences acting on both the extensor and flexor musculature of the forelimbs arising from the labyrinths, neck proprioceptors and from joint afferents.

The second problem lies in the area of the process of compensation following the loss of one labyrinth. The labyrinths are recognised to play an important role in the regulation of posture, as is easily demonstrable following the destruction of one labyrinth. Hemilabyrinthectomy results in marked postural deficits that render an animal incapable of carrying out coordinated movement. With time the symptoms diminish and an almost complete compensation to the insult occurs. The compensation is so complete that it becomes very difficult to distinguish between a normal and a hemilabyrinthectomized animal. The mechanism behind this postural compensation is poorly understood, (although a vast literature is available on compensation in the vestibular ocular reflex). In the early stages following hemilabyrintectomy it is intuitively apparent that the remaining labyrinth has inadequate control to stabilise the animal,however as time progresses this control is re-established. By experimenting with acute and chronic hemilabyrinthectomized cats it is hoped that a description of labyrinth and neck reflexes and their interactions will provide an insight into some aspects of the process of compensation.

Literature Review.

A perspective on the development of vestibular physiology.

1.1.0 The early history of labyrinth physiology.

Outline: The association of equilibrium with the labyrinth in the late 1800's and the challenge to previously accepted theories on labyrinthine function. The recognition of the adequate stimulus to the semicircular canals and the suggestion of a mechanism of sensory transduction. Breuer's functional separation between semicircular canal and otolith function.

The foundations of modern vestibular physiology can be traced to the second half of the nineteenth century. During this period the labyrinth was, for the first time considered as a sense organ concerned with equilibrium (Goltz, 1870). The evidence on which Goltz based this view followed from his observations on the behaviour of frogs following destruction of the labyrinths. Although not the first physiologist to observe disturbances in equilibrium following labyrinthectomy (Flourens (1824) almost fifty years previously had destroyed semicircular canals in pigeons), Goltz's theory challenged the established ideas on vestibular function. The structure and function of the semicircular canals and their close relationship with the cochlea had inspired theories in which the canals subserve

recognition of the different directions from which sounds originate. The protagonists of this theory argued that the disturbances in equilibrium seen by Goltz following destruction of the labyrinth resulted either from post-operative irritations, or cerebral lesions accompanying the destruction of the labyrinth or from the loss in the ability to localise sounds, (which would result in disorientation of the animals). Although the evidence behind this acoustic theory of canal function was largely anatomical, support at the time from the scientific community (Helmholst amongst them) was considerable (see review of A.Boettcher's monograph by E.Hart, 1873). The strength of the support for this theory insured its survival well into the twentieth century, (see Camis, 1930).

At the same time as Goltz was presenting his theory, Mach (1875) in Prague, Breuer (1874) in Vienna and Crum-Brown (1874) in Edinburgh independently proposed that the semicircular canals were involved in the perception of angular accelerations. The deductive reasoning behind this statement differs only slightly between all three authors. Crum-Brown (1874) in a communication to the Royal Society of Edinburgh described the effects of rotating a subject (with eyes closed) about an axis passing through the head. Convinced of the existence of a 'sense of rotation' Crum-Brown reported that with uniform rates of rotation the subject initially perceives the rotation but the effect diminishes with continued rotation until, with time, no sensation is perceived. On termination of rotation, the

subject experiences the sensation of rotating about the same axis as previously rotated, though now in the opposite direction. The initial perception of the rotation and the 'complementary apparent rotation' on stopping the spin were recognized as a consequence of the angular accelerations experienced at the start and the finish of the rotation. The only receptor system that could be thought to respond to angular accelerations were the semicircular canals. Crum-Brown argued that rotations about an axis normal to the plane of a canal would result in a flow of endolymph relative to the walls of the canal. The flow of endolymph was thought to cause the excitation of the nerve terminals in the ampulla. The stimuli to the nerve terminals during uniform rotations reduces as the relative motion of endolymph occurs initially as a consequence of its own inertia. This then explained why there is no perception of rotation at uniform rates. On rapid decceleration from uniform rotations the "contents" of a canal will carry on in the direction of the initial rotation, thereby producing the sensation of apparent rotation in the opposite direction. Due to the lack of knowledge regarding the excitation of nerves at this time Crum-Brown argued that, since canals could be paired on opposite sides of the head, accelerations would be signalled by one canal and deccelerations by the complimentary canal of an individual pair. The rationale behind this was that during rotation in the plane of a pair of canals, one canal would be ampulla leading the other ampulla trailing. Consequently the direction of endolymph flow relative to the ampulla at the

start and finish of a rotation would be different in both canals. Each individual canal was theorized to transmit the sensation of rotation about one axis and one direction only. The three pairs of complimentary canals were thought to be sensitive to any rotation about axes at right angles to their relative planes. This work provided a theoretical basis for a theory of operation on which experimental work could follow. The adequate stimuli to the canals had been recognised and a theory of sensory transduction in the canals (i.e., the flow of endolymph over nerve terminals in the ampulla) presented. Following on from the initial work of Crum-Brown (1874) and others, Breuer (1875, 1891) later differentiated in functional terms between the semicircular canals and the otoliths.

The otolith organs were thought by Breuer to contribute to the perception of linear accelerations, and as a consequence, to the position of the head with respect to gravity. Like the work on semicircular canals a mechanism of sensory transduction in the otoliths combined anatomical and physical quantities (Breuer, 1891). With the otoliths lying above the sensory epithelia of the macula it was suggested that during rectilinear acceleration the inertia of the otoliths would tend to leave them behind, and so cause bending of the imbedded cilia of the macula below. As the otoliths could be displaced in three dimensions all changes in head position were predicted to initiate a response.

Thus, in conjunction with the semicircular canals the otoliths were thought to enable perception of movement

and position of the head respectively. The work of Goltz, Crum-Brown, Mach and Breuer defined a new direction of thinking about the function of the semicircular canals and otolith organs despite continued support for the acoustic theory.

The new theory associating the labyrinth with equilibrium and orientation in space was strengthened by the clinical observations of Charcot (1874) (see also Hughlings Jackson 1874), in the course of his studies of the case histories of patients with Menière's disease and other disorders of equilibrium. Charcot established that the sudden attacks of giddiness and nausea, that characterise these diseases resulted from aural trouble, and not as previously thought to gastric or liver complaints. (The liver having previously been implicated as the diseased organ solely on the presence of bile in the vomit of patients with Meniere's disease.) Patients who suffer from Meniere's disease suddenly make violent jumping movements which can throw them with great force to the ground. During these seizures the patient experiences a sensation of a movement or translation of the body, or a rotation about some axis. The perception of these imaginary rotations is different in different patients but the resultant movements of these patients were taken by Charcot to demonstrate that the vestibular system can influence the motor system as well as consciousness. The importance of Charcot's studies lies equally in the fields of vestibular physiology and in the advancement of medical practice. The recognition of the inner ear as the source of the

disturbances associated with Meniere's disease resulted in more appropriate treatments of the disorder than was previously possible, simply by the recognition of the inner ear as the site of the disease. In addition the association of disorders of equilibrium with a pathology of the labyrinth aided the views of labyrinth function as professed by Goltz and others.

The theories of labyrinthine function presented by Crum-Brown (1874) were formulated to describe how a sense of perception of movement could exist and do not consider the vestibular system as a possible source of influences on muscle. Despite this, and following on from the work of Crum-Brown, Breuer and Goltz workers such as Edwald (a pupil of Goltz) and von Cyon investigated the possible motor function of the labyrinth. Edwald's (1896) contribution to an understanding of vestibular function is largely based on his belief that the semicircular canals exert a tonic influence on the tonus of skeletal muscle. His experiments, carried out on pigeons, are also of interest in relation to theories concerning the adequate stimulation of semicircular canals. Edwald developed a technique that produced mechanical stimulation of individual canals. By compressing a point on a membranous canal, Edwald was able to set up endolymph flow towards or away from the ampulla. Compression applied to the posterior canal resulted in head movements in the plane of the canal in a specific direction ,while decompression produced movements in the oppsite direction, though in the same plane. The results of these experiments are important in

several respects: (1) the demonstration that disturbance of the endolymph (possibly flow) can act as a stimulus to the nerve terminals in the ampulla of the semicircular canals, and (2) that this stimulation influences the behaviour of skeletal muscles (leading to movements of the head). In addition these experiments demonstrate that flow towards the ampulla influences the behaviour of neck muscles in one sense while flow away from the ampulla influences the behaviour of these muscles in an opposite sense. From this Edwald (1892) proposed that the flow of endolymph in one direction excited nerve terminals while flow in the opposite direction produced inhibition. To justify this he (Edwald, 1892) suggested that a constant "cilary action" of the hair cells within the semicircular canals resulted in a degree of tonic excitation of the muscles, which was then modulated by semicircular canal stimulation. Canals could therefore respond to rotations that were ampulla trailing or ampulla leading.

Using light pressure on the bony wall of canals von Cyon (1877) also stimulated individual semicircular canals. He showed that in rabbits and pigeons mechanical stimulation of canals produced pendular eye movements. These movements involved both eyes and were graded in terms of duration and frequency with stimulus intensity. These experiments also demonstrated that the direction of these eye movements was dependant on the canal stimulated. From the results of these experiments v.Cyon proposed that excitation of the labyrinths controlled "the distribution and strength of nervous activity" transmitted to the

voluntary muscles. Although he demonstrated such effects in the extraocular muscles, he does not appear to have sufficient evidence to expand this theory to encompass the rest of the skeletal musculature of the body as is implied in his writings.

In correlating reflex movements with the labyrinths Breuer (1875, 1891) had proposed that labyrinthine reflexes fell into two groups, one group associated with the semicircular canals and the other with the otoliths. Breuer's experiments examined the rotary and post rotatory reactions of the head and eyes of subjects in a revolving chair. He found that when the attitude of the head was altered a visual vertigo corresponding to the attitude of the head resulted. The rapid alternating eye movements (nystagmus) which brought about this vertigo were correctly associated with stimulation of the semicircular canals. The eye movements were considered to be reflexes that resulted from head movements.

As previously stated, Breuer (1875, 1891) had proposed that a group of static reflexes resulting from the position of the head, and originating from the otoliths existed. Among the observations which he considered to be manifestations of these reflexes were the characteristic head tilts seen in animals following unilateral labyrinthectomy, and the compensatory eye positions taken when the attitude of the head is changed. Breuer's insistence on a group of static reflexes originating from the otoliths was largely based on his theory of otolith function (Breuer, 1891) which at that time lacked

sufficient experimental support for general acceptance. The lack of experimental evidence for the existence of these reflexes is easy to understand when the inaccessibility of the organs in mammals is considered, and how little knowledge of its function was available. Unlike the semi-circular canals where mechanical stimuli could be applied directly to individual canals such stimulation could not be applied easily to the otoliths without inflicting damage to the canals, which, in itself, would result in postural disturbances. For these reasons the otoliths were largely neglected in early researches on the vestibular apparatus.

As the turn of the century approached, the vestibular apparatus (semicircular canals and otoliths) was being strongly associated with the control of equilibrium. However, despite the experiments of Edwald and v.Cyon the reflex reactions of skeletal muscle to stimulation of the labyrinths were not firmly established, and it was not until the investigations of Sherrington on decerebrate animals (Sherrington, 1898), and the subsequent observations of Magnus and his co-workers that a group of tonic reflexes were associated with the otolith organs.

1.2.0 The discovery of neck reflexes and the classification of labyrinthine reflexes.

Outline: The independent discovery of postural reflexes acting on the limbs and arising from the upper cervical region by Sherrington and Magnus. Subsequent study of neck

and labyrinth reflexes by Magnus and co-workers. Support for Breuer's classification of reflexes.

Sherrington in a paper published in 1910 (page 112) notes that head rotations about the long axis of the neck in a decerebrate cat inhibit extensor tone on the side of the lowered pinna and bring about active flexion of the knee. This behaviour persisted following section of both 5th and 8th nerves and deafferentation of the limb. This observation by Sherrington coincided with investigations of Magnus and de Kleijn (1912) on the reflex effects of head rotations. In a personnal communication to Magnus, Sherrington detailed his observations, and added that the effect was abolished after sectioning the first three pairs of dorsal roots of the cervical nerves (Magnus and de Kleijn, 1912 page 468; for English translation see Fulton (1951), page 177). Sherrington and Magnus's work taken together established that reflex changes in limb posture can accompany alterations of head position on the neck. Future experimentation into these observations was left by Sherrington for Magnus to carry out. These reflexes were not labyrinthine in origin, however, and their source became the subject of a careful series of experiments by Magnus and de Kleijn who recognised they originated from proprioceptors located in the neck.

It had been known for some years previously that section of the muscles of the back of the neck in dogs results in ataxia of gait and renders pigeons unable to fly (Bernard, 1858; Hughlings Jackson,1874). The demonstration

by Magnus that reflex movements of the limbs in a bilaterally labyrinthectomised cat result on rotation of the head, established the cervical region as an important site in the generation of postural reflexes acting on the limbs. These reflexes were called neck reflexes and their discovery coincided with the description of reflexes that were dependant on the integrity of the labyrinths. Investigations into these reflex systems were lead by Magnus and his collaborators culminating in the publication of Magnus's book "Korperstellung" (1924) two years before his death. English summaries of this work can be found in the Croonian and Cameron lectures (1925, 1926), and in the papers of de Kleijn (1923), de Kleijn and Versteegh (1927) and Dusser de Barenne (1934).

Magnus considered postural reflexes under three headings; 1) local static reactions, which tend to affect single extremities, 2) segmental static reactions in which influences from one extremity affect the crossed limb and 3) general static reactions in which more than one segment of the body takes part. The reflexes observed by Magnus arising from the labyrinths and the neck were ascribed to this third heading and in particular to a further subdivision of this group, the attitudinal reflexes. These attitudinal reflexes, best seen in decerebrate preparations on changes in head position, are manifest as a redistribution of tone in the muscles of the limbs and neck. As changes in head position result in a torsion of the neck and an alteration of head attitude in space, both labyrinth and neck reflexes will be brought into play

simultaneously. By taking these observations into account Magnus and de Kleijn undertook an investigation into each of these reflex systems separately.

Neck reflexes were studied without labyrinthine contamination by simply destroying both labyrinths. By doing this it was found that head rotations caused asymmetric changes in the extensor tone of the limbs. These reflex alterations in muscle tone are described as being tonic in nature, that is, they persist for as long as a certain position of the head on the neck is maintained. If the head is rotated about an axis such that the jaw points toward one side of the animal, then the extensor tone of the fore and hind limbs of that side increases whereas the tone in the opposite side decreases. With ventroflexion and dorsiflexion of the head the reflex responses change from the asymmetric pattern observed between limbs of the opposite sides (seen with rotations about the longitudinal axis) to a symmetrical pattern. Ventroflexion decreases extensor tone in the forelimbs and increases extensor tone in the hindlimbs, dorsiflexion producing the opposite response (that is extension of both forelimbs and apparent flexion of the hindlimbs). The above pattern of neck reflexes was found to be similar in most mammals except in rabbits where dorsiflexion results in extension of both fore and hind limbs, while ventroflexion leads to flexion of all four limbs. In general, neck reflexes result in opposite reactions in the musculature of different pairs of limbs (Magnus, 1926). The chin limbs extend with lateral rotations of the head. Magnus (1926) also described these

reflexes as having a characteristically variable latency, ranging from a third of a second to six seconds.

In conjunction with his description of neck reflexes Magnus also devoted considerable effort in describing reflexes of labyrinthine origin. Labyrinth reflexes were studied by Magnus in isolation from neck reflexes by either immobilizing the head, neck and thorax in a plaster cast or by sectioning the first three dorsal roots. By changing the position of the head in such preparations, the reflex response of the limbs can be observed. Like neck reflexes, changes in the position of the head of a decerebrate cat (with intact labyrinths) result in tonic alterations in the posture of the limbs. Magnus and de Kleijn (1912) reported that these tonic labyrinth reflexes affect all four limbs equally. With each position of the head in space a certain amount of extensor tone is assossiated with that position. Magnus and de Kleijn (1912) reported that the extensor tone is maximal when the animal is brought into a supine position with the snout 45 degrees above the horizontal, and is minimal with the animal in the prone position, the snout 45 degrees below the horizontal. Like neck reflexes, labyrinth reflexes were described as having long latencies varying from a quarter of a second to twenty three seconds. On bilateral labyrinthectomy the alterations in limb posture seen by changing the position of the head disappear, thus indicating that the labyrinths contribute to their production. Furthermore, the magnitude of these reflexes is independent of the initial angular accelerations

accompanying a positional change. The tonic reflex reflects only the static head position in space. From these observations it was possible for Magnus to conclude that these positional or "attitudinal" reflexes were not of semicircular origin, suggesting that the otoliths were responsible for their generation. Although evidence strongly supported the otoliths as the receptors involved in these tonic reflexes and hence strengthening Breuer's (1875) conception of labyrinthine function, the positive association of the otoliths with these reflexes was difficult to ascertain for the reasons discussed earlier (see page 11). Destruction of the otoliths (utricle and sacculus) was believed impossible in mammals without inflicting damage to the semicircular canals (though see page 22), though a non intrusive but nevertheless traumatic technique for rendering the otoliths non functional was developed. First described by Wittmaack (see de Kleijn and Versteegh, 1927; Magnus, 1926) the technique employs high speed centrifugation (1000 rpm) of anaesthetised guinea pigs. The centripetal forces developed detach the otolithic membranes from the maculae. This then produces a preparation with intact semicircular canals in which changes in head position do not alter the condition of hair cells of the macula. Magnus (1926), in describing such animals, states that all reflexes resulting from position were absent although transient refexes arising during changes in position were still present. The tonic reflexes are therefore of otolithic origin while the transient responses are presumably semicircular canal reflexes. This

scheme conforms to Breuer's two groups of labyrinth reflexes. The reflexes from the labyrinths are classified as either; I. Reflexes responding to movement, and II. Reflexes resulting from position. The above experiments positively identified the various components of the vestibular system with one group of reflexes. The tonic reflex including compensatory eye positions, labyrinthine righting reflexes (observed in high decerebrates) and the previously described reflexes acting on the limbs originating from the otoliths. Rotatory reactions such as nystagmus of the eyes and head along with the transient responses seen in the limbs were associated with the canals.

A further development of Breuer's ideas on the function of the otoliths and their activation came from Magnus's description of the tonic reflexes and the anatomical considerations of utricular and saccular positions in the head. With the head in a position where the tonic labyrinth reflexes are at a maximum, that is greatest extensor tone within the limbs, the otoliths are in a position where they pull on the utricular macula, this suggested to Magnus that maximal excitation of the macular epithelium results when the otoliths pull on it. Furthermore it was argued that the utricular macula was responsible for the generation of the tonic reflexes, the saccular macula seemingly not being involved. The latter was confirmed following the development of techniques that allow the sacculus to be removed without damage to the utricle or semicircular canals (see de Kleijn, 1923). This

operation was performed on rabbits who subsequently showed all labyrinthine reflexes, with no evidence of spontaneous vestibular disturbances (de Kleijn, 1923; de Kleijn and Versteegh 1927). From these experimental observations the conclusion was reached that the utricle was responsible for the observed tonic reflexes, and that maximal and minimal utricular excitation results when the otoliths are in positions that pull upon and compress the sensory epithelium respectively. De Kleijn and Magnus's (1921) observations suggested that tension or pull on the sensory hair cells of the macula was the effective stimulus in the generation of tonic labyrinth reflexes. Accordingly, and in agreement with the writings of Magnus, it is expected that movements of the head away from the minimal position (prone, mouth 45 degrees below horizontal) would result in utricular excitation independent of the direction of movement. Additionally Magnus (1926) claims that each utricle affects both ipsilateral and contralateral limbs equally, with no alterations of tonic labyrinthine reflexes on the limbs occurring following unilateral labyrinthectomy. Reflexes were observed to be symmetrical after ablation of one labyrinth (Magnus, 1926).

The ideas of Magnus and his collaborators were based on observations of limb posture following changes in head position. Despite the generality of Magnus's theories on utricular influences on the limbs, the published experimental protocols (Magnus, 1926) seem only to involve positional changes within the saggital plane. In addition,

Magnus made the important distinction between reflexes arising from stimulation of the otoliths, and those arising from the semicircular canals. The difference between the two systems of reflexes was in agreement with the original scheme of reflex actions suggested by Breuer (1898).

From a functional view point labyrinth and neck reflexes must be considered together. In Magnus's scheme of symmetrical labyrinth and asymmetrical neck reflexes the proposed co-operation between reflexes seen in the decerebrate preparation were thought to occur in the natural attitudes of intact animals during daily life. A movement of the head, for example, in which a cat raises its head to gaze upwards results in both labyrinth and neck reflexes. The assumed posture, i.e., extended forelimbs and flexed hindlimbs results from the algebraic sum of two reflex systems. The labyrinthine component is equal in all limbs, but the dorsiflexion of the neck resulting from the upward head movement leads to the adoption of an asymmetrical posture, which is characterised by forelimb extension and hindlimb flexion. Thus in Magnus's scheme the effects on the limbs come from two sources; (1) tonic labyrinth reflexes affecting the limbs directly, and (2) by neck reflexes resulting from the changing attitude of the head on the neck.

The theories of Magnus on vestibular function were widely accepted by the contemporary scientific community, and in consequence other workers investigating tonic reflexes discussed their results within the framework descibed by Magnus. Noteable in this respect, for example,

is the work of Beritoff (1914, 1915) on the reciprocal relations between antagonist muscles during labyrinth and neck reflexes. Working with decerebrate cats Beritoff (1914, 1915) reported that changes in head position relative to the trunk did not always result in a change in the tone of the limb muscles. However, in the absence of a tonic reflex the presentation of some form of peripheral stimulation resulted in the release of the reflex. Although Beritoff's experimental protocols show that both labyrinthine and neck influences must be altered to some extent during any of the positional changes used, little attempt was made to experimentally isolate one reflex from the other. Beritoff apparently, preferred to rely on the results of Magnus in the discussion of his own findings. In consequence the results concerning labyrinthine actions are difficult to assess as there is contamination from neck proprioceptive input. In one experiment, however, Beritoff destroyed both labyrinths. The results from this experiment show that twisting of the neck produces reciprocal changes in the activity of antagonist forelimb muscles. The direction of response confirmed Magnus's scheme of neck reflexes.

Magnus's description of tonic labyrinthine reflexes formed the basis for a number of investigations, the acceptance of Magnus's acounts of these reflexes, however, resulted in most workers looking, as Beritoff did, at only two different static head positions when examiming positional reflexes. These positions corresponded to the position of maximal and minimal extensor tone. Denny-Brown

(1929) investigated the effect of labyrinth and neck reflexes on red and pale muscles in this way, showing that the tonic reflexes are most prominent in the deep red muscles. Similarly, Pollock and Davis (1930a) in comparing their anaemic decerebrates with the Sherringtonian decerebrate preparation used the reflex scheme of Magnus in highlighting the similarities and differences between the two preparations. Several studies on labyrinth reflexes, however, demonstrated that under certain circumstances the scheme of reflexes described by Magnus could not explain their observations.

1.3.0 The problems associated with Magnus's scheme and the experimental evidence against it.

Outline: Recognition of functionally inappropriate labyrinth reflexes for some postural disturbances. The experiments of Tait and McNally suggestive of asymmetrical pattern of reflexes. Contributions to the controversy found in the work of Rademaker and Dusser de Barenne on tilt and rotary reactions of animals.

A symmetrical form of reflexes originating from the labyrinths on strictly functional terms fails to provide an animal with the capability to stabilize equilibrium during most situations following a disturbance of head position, or during voluntary changes in head position. For example a quadruped standing on a platform which is tilted about any horizontal axis will in Magnus's scheme of symmetrical

reflexes show equal changes in tone in all four limbs. Such behaviour could reasonably be expected to result in postural changes that do not compensate for the redistribution of weight over the support area, and so could result in a situation in which the equilibrium of the animal would be threatened.

Departures from Magnus's symmetrical scheme of reflexes were first observed in the behaviour of animals subjected to static positional changes or to rotatory tests. Tait and McNally (1925a, b) showed in frogs, that rotations about a longitudinal axis resulted an asymmetric posture of the limbs. On slow rotation to the right, about a longitudinal axis a simultaneous extension of the right forelimb and flexion of the left forelimb was observed. These compensatory reactions, persisted when the animal was held continuously in a tilted position. On rotation toward the left the postures of the limbs altered, the left forelimb becoming extended and the right forelimb flexed. Following total ablation of all six ampullae (Tait & McNally, 1925b) the above responses can still be observed, but on destruction of the otoliths these reactions are lost. Furthermore, saccular ablation in an otherwise intact frog does not affect these "gravity responses", Tait and McNally concluded that the observed compensatory reactions were dependent on the utricles (Tait & McNally, 1925b).

Asymmetric reactions to rotatory movements had been previously reported by Dusser de Barenne (1918), who did not test static positions. Dusser de Barenne (1918) reported that if a frog is suspended vertically by a thread

and a twist applied so as to initiate rotation slowly about the longitudinal axis the hindlegs assume an asymmetrical position. For example, rotation to the left results in abduction and extension of the right leg while the left leg becomes flexed at the knee. As the direction of rotation reverses, as a result of the thread untwisting itself, the attitudes of the limbs also become reversed. These responses were shown to be dependant on the integrity of the labyrinths. These reflexes were not equivalent to the static reflexes reported by Tait and McNally (1925a), but would appear to originate from stimulation of semicircular canals, particularly, the vertical canals. Rademaker (1935) also reported the appearance of similar reflexes to those described by Dusser de Barenne. By exposing animals (mainly dogs) to rotations in a horizontal plane Rademaker demonstrated asymmetric reflexes of labyrithine origin that were dependant on direction of rotation. Rademaker, more importantly, observed that passively tilting the support surface of a blindfolded animal, standing with longitudinal axis parallel to the axis of tilt, resulted in extension of the downhill limbs and flexion of the uphill limbs. The passive displacement of the animal leading to the adoption of attitudes that stabilize the trunk. The ability to compensate for changes in the support surface is lost following bilateral labyrinthectomy. The reactions observed by Rademaker were made on intact animals. Investigating labyrinth reflexes, and in particular tonic reflexes in decerebrate preparation, Rademaker noted that whole body rotations of small amplitude about a fronto-occipital axis

were ineffective in augmenting electromyographic (EMG) activity from biceps or triceps of the forelimb. But on reaching a position 80-90 degrees from the normal a marked facilitation in EMG of both muscles was observed. With rotations beyond this it was noted that this augmentation of rigidity decreased, the amplitude of the EMG progressively diminishes as the upside down position was approached. Two features of this work are important. First, on moving from the mimimal to maximal positions of Magnus and de Kleijn, the EMG passes through a period of maximum activity corresponding to when the animal is in the lateral position (half way between minimal and maximal positions). Second, triceps and biceps become coactivated on moving from a normal to a lateral position (see Rademaker, 1935 Figs. 88 and 89). Similar results were found on rotations about a bitemporal axis, the maximal activity occurring at some point midway between the positions of "maximal" and "minimal" tone. Rademaker does not indicate which side he was recording from, and therefore does not note whether the reactions of both forelimbs during lateral rotations were the same. What he was clear about, however, was that his results did not agree with those of Magnus, nor with the conclusions of Beritoff (1915) concerning the reciprocal form of labyrinth reflexes. Although aware of the differences seen between his own work and that of Magnus (1926), Rademaker (1935, page 180) suggested that (perhaps) these differences may be attributed to some fault in his (Rademaker's) experiment. Rademaker concluded that the absence of a difference in EMG activity at the minimal and

maximal positions was a consequence of either adaptation or fatigue in the muscles, rather than accept the conclusion that the reflex scheme described by Magnus may have been incorrect. In disagreement with Beritoff (1915), Rademaker maintains that Beritoff's experiments concerning the role of extensors and flexors during tonic labyrinth reflexes are misleading due to the reasons of contamination from neck reflexes (see earlier for more detailed information). Rademaker's results suggest that coactivation of flexors and extensors is the predominant pattern during tonic labyrinth reflexes, rather than one of reciprocating activity. The combined works of Rademaker (1935) and of Tait and McNally (1925a, b) on both intact and decerebrate preparations, despite a reluctance to openly contradict Magnus's theory of labyrinthine reflexes and otolith function, reveal several features that cannot be explained by the widely accepted views of the time. The major concern was that lateral tilts away from normal, and therefore displacements of the utricular otoliths, do not result in attitudinal limb reflexes that conform to a theory of utricular function in which movements in any direction out of the normal result in excitation.

1.4.0 New techniques and a new approach to theories on labyrinth reflex behaviour.

Outline: Adrian's experiments recording from brainstem neurones responsive to tilt. The description of different classes of reponse. Utricular nerve recording by Lowenstein

and Roberts and the presentation of a scheme of reflex function based on their recordings. Theoretical consideration of otolith and neck reflex interaction by von Holst and Mittlestadt. The differences between the models of Lowenstein and Roberts and of von Holst and Mittlestadt.

Adrian (1943) recorded single vestibular unit activity from the vestibular nuclei of decerebrate cats. Two classes of response were found. One group of units were shown to be responsive to angular accelerations, while a second group exhibited an output dependant on the position of the head in space. The units responsive to angular accelerations showed the following features: most possessed a resting discharge and showed bidirectional responses to positive and negative angular accelerations. Rotations in the plane of a particular canal resulted in either an increase or a decrease in the firing rate of responsive units. Thus ampulla leading and ampulla trailing accelerations were both recognized as effective stimuli for the semicircular canals, these observations agreeing with Edwald's (1896) theory of canal function. [From these results, and those of Steinhaussen (1933), who had demonstrated that the cupula extended across the ampullary swelling it was recognised that the endolymph and cupula form a rigidly coupled system, the dynamics of which approach those of a highly damped torsion pendulum (Steinhausen, 1933; Van Egmond, Groen & Jongkees, 1949).]

The demonstration of a resting discharge from the canals did not conform to the most accepted theories of

vestibular function. In Magnus's (1926) theory, all resting activity from the vestibular system resulted from the weight of the otoliths upon the sensory macula - this activity in turn contributing to the maintenance of tone in various muscle groups. Clearly, in the light of Adrian's result the resting output from the canal sensitive units could also be considered to contribute to the maintenance of tone.

A further objection to Magnus's theory resulted from the behaviour of units described by Adrian to be gravity receptors. These units displayed responses that were dependant on the position of the head relative to the vertical and also showed sensitivity to linear accelerations. On lateral tilts of the head all units showing position sensitivity displayed an increase in firing on lowering the recording site (side-down), and a decreased rate with opposite tilts (side-up). Adrian reported that this type of unit could be found relatively easily but units responding to tilts about a bitemporal axis were very difficult to locate. Of the units showing a response to lateral tilts all displayed an increased output when subjected to linear accelerations away from the recording side. This behaviour indicates that such accelerations have the same effect on these cells as a gravitational pull toward the recording side. Gravity responsive units all increased discharge rates with tilts in one direction, with the discharge being reduced or silenced with tilts in the opposite direction. These results reveal a further possible problem with Magnus's

interpretation of otolith mechanics. In Magnus's scheme utricular units may be expected to increase discharge rates with any direction of movement away from the normal and not show an asymmetric response to opposite direction of tilts as found by Adrian. Adrian (1943) recorded from the brain stem of decerebrate cats in the vicinity of the vestibular nuclei, consequently, the majority of his recordings will have been from secondary neurones, and the results may only be indicative of the response dynamics of the vestibular otolith system, and therefore does not constitute a complete case against Magnus.

Lowenstein and Roberts (1950) described the primary afferent responses to tilt from the isolated otolith organs of the thornback ray. Lateral and fore and aft tilts were employed. Recording from utricular and saccular afferents it was found that most units responded to fore and aft tilts as well as lateral tilts. The units capable of carrying a position dependant signal -the static position receptors- all showed, on maintained lateral deviations from the normal, a decreased activity with side-down tilts and a maximum output in side-up positions. (Side-up tilts were defined as lateral rotations which acted to raise the recording site, while side-down tilts correspond to lateral tilts which lowered the recording site.) The majority of these units were located laterally on the macula surface. Of this population of units some also responded with an increased discharge with nose-up tilts and a decreased discharge with nose-down tilts, while others responded oppositely to such tilts. Thus two groups of sense endings

were described, one responding with an increase in discharge to combinations of side-up and nose-up displacements, the other to side-up and nose-down displacements. From this result it was deduced that the appropriate stimuli to the neuromast cells is a medial deflection of the otolith organs. And, following from this it was further suggested that the side-up, nose-up receptors ought to be located in the anterio-lateral portion of the utricular macula and the side-up, nose-down receptors in the postero-lateral portion of the macula.

In addition Lowenstein and Roberts (1950) argued that if -as had been suggested by Breuer (1898) and subsequently by Magnus and de Kleijn (see de Kleijn, 1923; Magnus, 1924, 1925, 1926)- a permanent association between certain macula areas and groups of effector muscles existed, then the otoliths are chiefly concerned with the control of the contralateral antigravity muscles rather than exerting an equal influence bilaterally as implied by Magnus's scheme (1926). The anterior and posterior macula areas were thought to influence hind and, forelimbs respectively. In their hypothetical scheme Lowenstein and Roberts (1950) assumed that the action of the otolith organs were antagonistic to the action of the ipsilateral vertical canals. The canals were thought of as a facilitatory influence acting ipsilaterally while the otoliths acted contralaterally. This model of labyrinth function requires that during lateral tilts an asymmetric pattern of reflexes results between left and right sides, while on fore and aft tilts there would be asymmetry

between the fore and hind limbs. The mechanics of such a scheme are outlined below and a diagramatic representation of this model is illustrated in Fig. 1. Lateral tilts to the left bring the utricle of the right and left sides to side-up and side-down position respectively. The right utricle (from the results of Lowenstein and Roberts (1950)) will exhibit an increased afferent output while the left utricle will show a decreased discharge. For the same direction of movement the output of the left anterior and posterior vertical canals will show a decreased firing rate. (The vertical canals had, as described previously, though in different species, been shown by Dusser de Barenne, 1918 and Rademaker, 1935 to play a role in the production of asymmetric limb postures.) The consequence of this activity, based on the hypothetical wiring scheme of Lowenstein and Roberts (see Fig. 1), would be that the antigravity muscles of the left fore and hind limbs would receive facilitation from the right utricle and from the left vertical canals. The equivalent muscles of the right side behaving reciprocally as a consequence of the activity patterns in the left utricle and the right vertical canals. On tilting in the fore and aft direction differential reponses were believed to occur between the anterior and posterior regions of the utricles, and between the vertical canals. On tilting forward the posterior regions of the utricles and the anterior vertical canals exert facilitatory influences on the extensors of the forelimbs, simultaneouly the hind limbs show a diminution of extensor tone resulting from decreased output from the anterior

Lowenstein & Roberts, (1950).

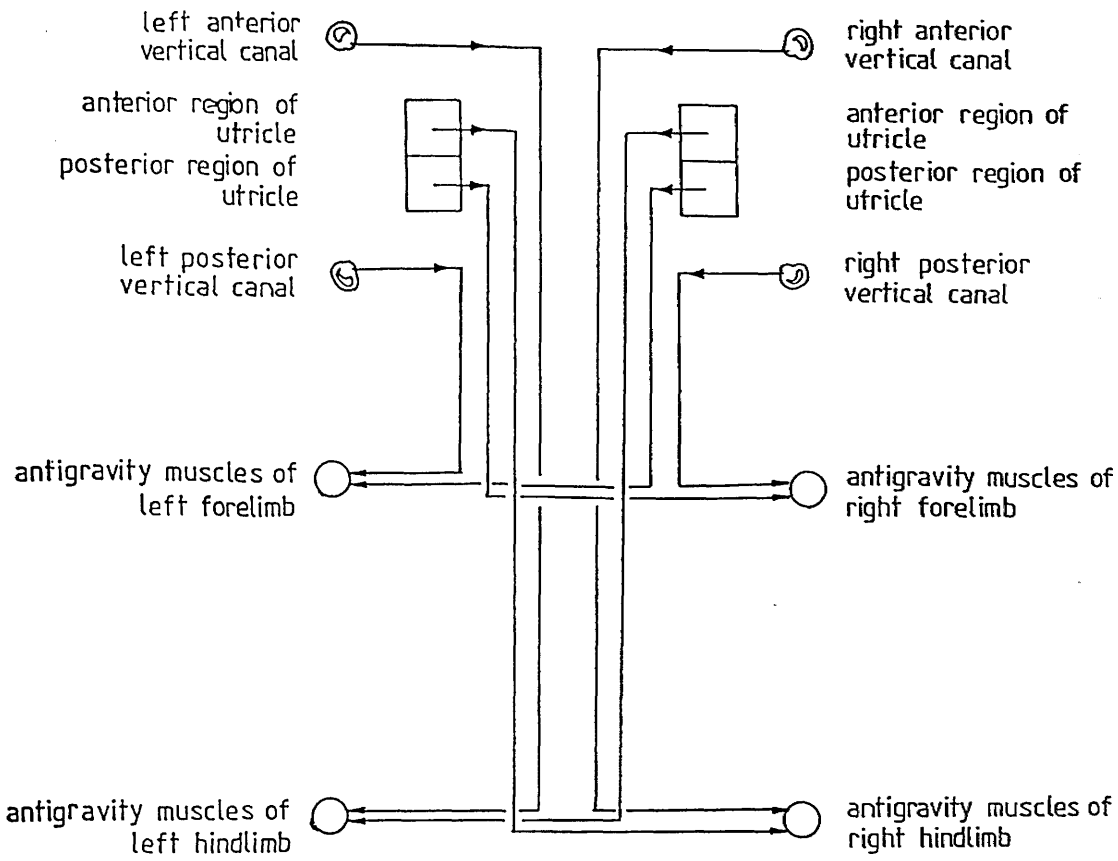


Figure 1. Model of the organisation of labyrinth reflexes as proposed by Lowenstein and Roberts (1950) and adapted from their original figure. With lateral tilts the canals which are rotated side-down increase their discharge, whereas the otolith receptors decrease output with side-down tilts. An asymmetric reflex organisation results from a proposed ipsilateral canal-antigravity muscle connection and a contralateral otolith-antigravity muscle connection.

utricular regions and the posterior vertical canals.

A necessary requirement of any model is that it should predict the outcome of a disturbance to the system it models for a wide range of experimental observations. One necessary condition that the Lowenstein and Roberts (1950) model must predict is the experimental finding that following hemilabyrinthectomy greater tone develops on the side of the intact labyrinth. For the model to fulfil this requirement it is necessary that the semicircular canals exert a greater influence over the muscles than the otoliths do.

An interesting point concerning this scheme is that as the tone resulting from the remaining semicircular canals is a consequence of the resting discharge of the canal afferents it will not alter between various static head positions. The output from the remaining utricle will however still show static sensitivity and therefore the tonic reflexes on the side of the lesion should remain almost unchanged following hemilabyrinthectomy. This last point was not made by the authors (Lowenstein anb Roberts, 1950), but is a necessary consequence of their model. The mechanics of this theory, based on the behaviour of primary otolith afferents, and the assumption of specific links between the labyrinth and antigravity muscles is in essence a modification of Edwald's (1892) theory of semicircular canal function and of Breuer's (1898) ideas on otolith function.

The concept of asymmetrical reflexes required by this model, although having been reported by several groups

(Tait & McNally, 1925a, b; Tait, 1926; Rademaker, 1935) was not widely accepted. Also the idea of a contralateral predominance of otolith influences was based soley on the finding that all the afferents tested showed an increased discharge with side-up tilts. This finding is in direct opposition to Adrian's (1943) results, and to the conclusions of other authors whose own results suggested either ipsilateral (Tait & McNally, 1925a, b; Tait, 1926) or bilateral (Magnus, 1926) influences from the otoliths. Despite these problems the importance of the Lowenstein and Roberts (1950) model is that it proposes the existence of asymmetric reflexes in direct contrast to the reflex scheme of Magnus (1926).

In the same year as the appearance of the Lowenstein and Roberts (1950) paper von Holst and Mittlestaedt (1950) published a theoretical model of postural control in higher vertebrates (including man),(see collected writings of von Holst (1973) for English translation). In this model two different sets of afferent signals, one from the labyrinth and the other from proprioceptors located in the neck, interact to maintain equilibrium. The afferent signals arising from the labyrinth and neck are regarded in the von Holst and Mittlestaedt (1950) model as being antagonistic to one another. If, for example, the whole body of an animal is inclined to one side, the limbs of that side will exhibit an increased extensor tone while the limbs of the opposite side will become flexed. The compensatory movements following such a tilt are the same as predicted by the

Lowenstein and Roberts (1950) scheme. However, if neck reflexes are considered the posture adopted by the limbs on tilting the head in a labyrinthectomized animal is opposite to that described above. In von Holst's and Mittlestaedt's (1950) model a rotation of the head either passively or actively in an intact animal results, as would be expected, in the production of both otolith and neck reflexes. The pattern of interaction, presented in this model, results in no alteration in limb posture, the opposing reflex actions summing together. Thus, it is argued that during active or passive movements of the head no sign of limb reflexes occur. The interaction between otolith and neck reflexes takes place as though there was a single receptor system located within the trunk itself. The von Holst and Mittlestaedt model (1950) like the model presented by Lowenstein and Roberts (1950) proposes an asymmetric pattern of otolith limb reflexes, however, von Holst and Mittlesteadt (1950) assume a predominantly ipsilateral action of the otoliths on the limbs, and consequently a contradiction arises in the discussion of these two views on labyrinthine reflexes. The two models are not, therefore, compatible.

In one model (von Holst and Mittlestaedt, 1950) facilitation of ipsilateral extensor tone arises from the ipsilateral otolith organs, while in the other model (Lowenstein and Roberts, 1950) the facilitation is believed to arise from the contralateral otolith. From a functional viewpoint the von Holst and Mittlestaedt model requires that the majority of ipsilateral otolith afferents should

show an increased discharge with side-down tilts. The opposite response is required in the Lowenstein and Roberts model (1950). The experimental basis behind von Holst and Mittlestaedt's concept of otolith function and reflex interaction is outlined below. Some of the evidence presented to support their model is based on the work of Griesmann (1922) and of Fisher and Wodak (1922) who investigated the reflex reaction in human limbs in response to hot compresses placed on the mastoid process. The results of these experiments may be difficult to interpret, since one cannot unambiguously identify the receptor giving rise to the limb reflexes. Caloric stimulation as used in the classical sense is well known to produce semicircular canal stimulation but its action on the otoliths is not known. The model of von Holst and Mittlestaedt (1950) like that of Lowenstein and Roberts (1950) is based on incomplete evidence for the existance of asymmetric otolith reflexes.

Although the two models differ in a mechanistic sense the proposed pattern of labyrinth reflex activity from each model offers a system of postural control which can function over a wide range of circumstances, unlike the limited model of Magnus. Interactions between the proposed asymmetric otolith and neck positional reflexes proposed in the von Holst and Mittlestaedt (1950) allow the head to move freely without threatening equilibrium, but during a postural disturbance the independent expression of labyrinth or neck reflexes can act to compensate for the disturbance. This interactive pattern of reflexes as first

suggested by von Holst and Mittlestaedt is therefore fundamentally different from the interactions that Magnus theorized to occur between labyrinth and neck postural reflexes.

1.5.0 The description of asymmetric labyrinth reflexes and their interactions.

Outline: Inconsistencies in published data with the Magnus scheme of reflex action. New techniques introduced by Roberts (1963) allow utilisation of independent labyrinth and neck stimulation in the study of labyrinth and neck reflexes. Asymmetric length changes are recorded in forelimb extensors by Lindsay, Roberts & Rosenberg (1976) during natural labyrinth stimulation. The scheme of reflexes described provide an experimental basis for previously proposed models of postural control. The experiments of Schor and others suggest contralateral otolith reflexes. Proposals as to the site of interaction of labyrinth and neck afferent systems.

Although Dusser de Barenne (1918), Tait and McNally (1925a) and Rademaker (1935) had demonstrated that asymmetric reflexes could be observed, the views of Magnus remained generally unchallenged and formed the standard text book view (Mountcastle, 1974, 13th edition). The 1950 models of labyrinthine function proposed by Lowenstein and Roberts and by von Holst and Mittlestaedt challenged the accepted theories, but could only partly justify their

descriptions with the experimental evidence then avaliable.

The unresolved issues were (1) what is the reflex behaviour of the limbs under natural stimulation of the labyrinths and neck, (2) how does this relate to otolith or semicircular canal function, (3) are the pathways ipsilateral, contralateral or bilateral and (4) what is the nature of the interaction of positional labyrinth reflexes with neck and other postural reflexes.

Examination of the published figures in a study on the interaction of vestibular reflexes with stretch reflexes by Koella, Nakao, Evans & Wada (1956) reveals features in their tension records which indicate asymmetric labyrinth influence. This result went unnoticed by the authors. The experiments investigate stretch reflexes in decerebrate cats at various angles of tilt about a longitudinal axis (0 prone, 60, 120, 180 supine, 240 ,300 degrees). Discussing their results with reference to Magnus, Koella et al. (1956) conclude that the stretch reflex is conditioned by the labyrinth with the larger stretch reflex occurring in the supine position rather than the prone position. What the authors miss, however, is that, althougth the stretch reflex peaks at around 180 degrees when stretches at 60 degrees are compared to those at 300 degrees, there is a marked difference in the amplitude of their peaks at the two different positions. On moving from 360 degrees to 300 degrees, there is an increase in the size of the stretch reflex, this increase is still evident on moving from 300 to 240 degrees. In Magnus's scheme this is not unexpected as the cat is being

moved toward the position of maximum tonus. On completion of the cycle through 180 to 120 degrees then moving from 120 to 60 degrees and then 60 to 0 degrees a reduced stretch reflex can be seen on moving toward 60 degrees, but on reaching 0 (360) degrees the reflex response increases (see figs 2 and 3 Koella et al., 1956). Considering reflex responses around +/- 60 degrees about the prone position the figures illustrate ascending levels of facilitation from 60 to 0 degrees and then to 300 degrees. In this respect the figures suggest the existence of an asymmetric labyrinth reflex interacting with stretch reflex pathways. One cannot deduce if side-up or side-down tilts give increased or decreased stretch reflexes as the side of the recording limb is not mentioned. The tension records show that the tension throughout the experiment (i.e. the records show continuous tests of the stretch reflex at different head angles), despite changes in position remains constant, implying that no direct influence onto the recorded muscle resulted from the positional changes. In this respect the experiments conform to Beritoff's (1914) description of labyrinthine influences becoming evident following peripheral stimulation.

In 1963 Roberts introduced a decerebrate preparation in which neck reflexes were isolated from labyrinth reflexes by denervating the first two intravertebral joints. Neck reflexes, having previously been demonstrated to arise from the receptors located in and around the first three cervical joints (McCouch, Deering and Ling, 1951), were therefore not evoked on head

movements with movement restricted to regions above the axis vertebra. Initially concerned with labyrinthine influences on the hindlimb, Roberts (1963) demonstrated that nose-up tilts of the head produced a facilitation of extensors of the hindlimb (revealed by shifts in tension/length plots of fluctuating cycles of applied tension and of applied length). With nose-down tilts a disfacilitation was observed. Such reactions conform to Magnus's description of labyrinthine action on the hindlimbs and as expected from this would act in opposition to neck reflexes evoked in an intact preparation with nose-up or nose-down tilts. The symmetry between hind and forelimbs which Magnus predicts was not tested for in these experiments, nor was the effect of lateral tilts.

Using the same preparation as Roberts, Gordon (1964) investigated labyrinth action on anconeus, an extensor of the forelimb during lateral and sagital tilts. Before preparing the limb for myographic recording it was noted that nose-down rotations resulted in forelimb extension and nose-up rotations produced flexion, on tilting side-down an asymmetric response was observed in the forelimbs. The ipsilateral limb becoming extended. Once the limb was prepared for recording, however, no responses (or in one case no consistent responses) could be obtained on lateral tilting, though lengthening and shortening were recorded in some instances following nose-up and nose-down rotations respectively. This observation conformed to the scheme of reflexes suggested to occur following nose-up and nose-down tilts by Lowenstein and Roberts (1950). The

forelimb extensor (anaconeus) contracting on movements (nose-down) that produced relaxation in hindlimb extensors (Roberts, 1963).

In a further treatise on labyrinth reflexes Roberts (1967) discussed the Lowenstein and Roberts (1950) hypothetical scheme of labyrinth reflexes in relation to their interactions with neck reflexes. As in von Holst and Mittlestaedt's (1950) model Roberts proposed pattern of reflexes results in actions that oppose tonic neck reflexes. The similarities between the reflex schemes is very strong despite different methodological approaches. The relationship between the two sets of reflexes in the intact animal allows voluntary movements of the head to be carried out without reflex constraint. Based on the experimental results obtained by nose-up and nose-down tilts a scheme of reflexes conforming to the proposed set of postural reflexes of Lowenstein and Roberts (1950) were described. In this scheme the symmetrical labyrinth reflexes of Magnus are replaced by asymmetry between fore and himdlimb labyrinth reflexes which interact with neck reflexes during movements of the head in such a way as to maintain stability.

Nagaki (1967) reported alterations in the integrated EMG of triceps brachii on subjecting decerebrate cats to whole body rotations about a longitudinal axis. The alterations in EMG could only be seen following spinal cord section at T12. Nagaki's results were based on experiments from 14 cats and showed 3 types of response to side-down rotations. In the majority of cases the

ipsilateral triceps showed an increase in activity with side-down rotations (54%). Though it was commonly found that side-down rotations resulted in either a decrease (32%) or no change (14%) in the integrated EMG activity of the ipsilateral triceps. Concerning the response to side-up rotations all triceps muscles from the 14 cats exhibited a decrease in activity. None of these responses conform to Magnus's scheme of positional reflexes, a point which was overlooked by Nagaki, (although the author cites Magnus (1926)). Following section of the first three cervical roots rotation of the head alone produced similar EMG changes in triceps as had been seen with whole body rotations. Nagaki believed that facilitation of extensor motoneurones occuring during side-down tilts of the head arose from the ipsilateral otolith, in agreement with von Holst and Mittlestaedt's (1950) hypothesised scheme of labyrinth reflexes and supported by Adrian's (1943) observations on central vestibular units.

Following hemilabyrinthectomy the contralateral reflexes become reversed. In order to explain these results, in respect to an ipsilateral drive from the otoliths, Nagaki theorised that side-up tilts (which in Adrian's scheme would silence the tonic activity of the remaining otolith) had to be altered centrally from a previously facilitatory influence to a bilateral inhibitory influence. In this scheme side-down tilts would increase vestibular drive, so causing an inhibition of left and right spinal extensor motoneurones. With side-up tilts the vestibular drive is reduced and a release of inhibition

bilaterally results in increased extensor activity of both sides. The spinal mechanism responsible for the switch between a previously facilitatory influence to an inhibitory one was purely hypothetical. However, the same result could be explained without this central switching from the reflex scheme of Lowenstein and Roberts (1949) and Roberts (1967). The decisive factor between the two possible explanations rests in the afferent response of the otoliths, and on the central pathways responsible for the reflex.

In a study on modifications of stretch reflexes Roberts (1970), see also Borland (1970), using the preparation introduced in 1963, reported alterations in the tension/length diagrams of extensors that are suggestive of an asymmetric labyrinth influence. With these results Roberts (1970) again emphasised the significance of the interactions between labyrinth and neck reflexes.

Ehrhardt and Wagner (1970) studied the effect of natural labyrinthine stimulation on hindlimb flexor and extensor motoneurones of decerebrate cats. Rotations were performed under conditions in which no elimination of neck reflexes had taken place and secondly after a pharmacological block of C1-C3 spinal roots. In experiments where neck reflexes were evoked simultaneously with labyrinth reflexes a small brief facilitation was observed during the head tilt, there was however no response to maintained position. The brief response seen in extensor motoneurones was lost following elimination of neck afferences. Ehrhardt and Wagner (1970) suggested the

existence of a neck reflex with a kinetic component much like that of the semicircular canals. Reflexes to maintained positional changes were seen immediatly after C1-C3 block. Extensor motoneurones were facilitated with both ipsi- (side-down) and contralateral (side-up) rotations. The intensity of the response was however always greatest in the ipsilateral limb. Ehrhardt and Wagner (1970) observed that most flexor motoneurones were inhibited by tonic labyrinth reflexes, although they suggest a synergistic pattern of activity may occur between flexor and extensor in some instances. Ehrhardt and Wagner's (1970) observations support both the theories of von Holst and Mittlestaedt (1950), and of Roberts (1967) in that labyrinth reflexes are not apparent while neck reflexes are simultaneously acting. With respect to the pattern of reflex activity onto hindlimb motoneurones, although left and right extensors receive facilitation there appears to be an asymmetry between the level of facilitation to the opposite extensors, the level of facilitation was observed to be greatest within the ipsilateral limb. The slight facilitation in the contralateral extensor cannot be predicted from the existing theoretical models of vestibular postural control and is not consistant with the results of Nagaki (1967), who reported a decrease in the EMG of forelimb extensors with side-up (contralateral) rotations. From the observations on flexor motoneurones it is difficult to reconcile their response to a functionally significant role in postural control. The often cited response to lateral

rotation is the production of flexion in the contralateral limb, but this is not seen in these experiments. What is observed, however, is a more marked extension ipsilaterally, with contralateral extensor tone increasing slightly above its normal discharge, but remaining less than that of the ipsilateral limb. These responses are obtained on tilting the head 90 degrees away from normal, and must result in marked torsion about the neck, despite the C1-C3 block some other cervical afferents from lower regions and cutaneous rsponses to stretching of the skin round the head and neck may have contributed to participation of other receptors in the observed responses. This possiby also exlaining the differences seen in comparison of Nagaki's (1967) results on the forelimb to those of Ehrhardt and Wagner (1970) on the hindlimb.

Strong support for an asymmetric pattern of labyrinth reflexes was provided in an investigation of tonic labyrinth and neck reflexes in decerebrate cats by Lindsay (1975). The papers published in connection with this thesis demonstrated the asymmetry and antagonism between labyrinth and neck reflexes (Lindsay & Rosenberg, 1973; Rosenberg & Lindsay, 1973; Roberts, 1973; Lindsay et al., 1976.).

Working with the preparation introduced by Roberts (1963), independent labyrinth and neck reflexes were evoked by head tilting and rotation of the axis vertebra, respectively, after the first and second cervical roots had been sectioned. In this preparation it was therefore possible by restricting movement of the axis vertebra to

elicit labyrinthine reflexes in isolation from neck reflexes. The two reflex systems then could be studied in isolation or together by rotating the head or the axis vertebra separately or together. By recording length changes in the medial head of triceps brachii (an extensor of the forelimb) during head or neck rotations asymmetries in the reflex behaviour were clearly seen.

On rotating the head to one side (approx 30 degrees) and holding a deviated position there is a shortening of triceps on the side to which the vertex is rotated (side-down), and a lenghtening in the corresponding muscle of the opposite side (side-up). These length changes lasted for the duration of the head deviation, muscle length returning toward its previous resting length on returning the head to its normal position. This pattern of tonic activity seen during side-down and side-up rotations was the most commonly described pattern of activity. Out of 30 decerebrate preparations displaying reflex actions the following results were obtained. With side-down rotations 59.3% of muscles showed an increase in activity (ie shortening), with 13% showing the opposite response (ie lengthening), the remaining muscles tested displayed either phasic (3%) or phasic/tonic (14.3%) increases in activity or phasic (1.9%) and phasic/tonic (0.5%) decreases in activity. In 17% of the muscles tested with side-down rotations no responses were recorded. With side-up rotations tonic lengthening of triceps was seen in 65.4% of cases, 2.0% displaying a shortening. Muscles displaying a phasic or phasic/tonic lengthening accounted for 2.0% and

10.7% respectively of observations made with side-up rotations. Contractions of a tonic, phasic and phasic/tonic nature were seen in 21.0%, 1.8% and 0.8% of cases respectively with this rotation. Side-up rotations in 17.3% of cases resulted in no reflex being observed. The majority of observed reflexes are clearly tonic or phasic/tonic in nature, displaying increased activity with side-down rotations and a decreased activity with side-up rotation. A phasic component in these reflexes is probably a semicircular canal phenomena, although it is also likely that it could result from otolith units showing dynamic discharge characteristics. The otoliths are considered the receptors responsible for the tonic nature of the reflexes.

Rotation of the axis vertebra resulted in neck reflexes, these reflexes were demonstrated to be antagonistic to the labyrinth reflexes described above. Side-down rotations resulted in a lengthening of triceps and side-up rotations resulted in shortening. By superimposing a neck reflex upon a previously evoked labyrinth reflex the muscle returned toward its resting length during the period of neck activation. On returning the neck to the normal position the previously evoked labyrinth reflex is again revealed. In this type of demonstration of antagonism between reflexes the dorsal roots of C1 and C2 were cut, if however the dorsal roots were left intact there is no response to head rotation. This demonstration of asymmetric labyrinth suppression by the simultaneous activation of neck reflexes is in agreement with the proposals of von

Holst and Mittlestaedt (1950, see also Mittlestaedt 1964) and later Roberts (1967, 1973) who had on theoretical grounds described such interactions between labyrinth and neck reflexes (see earlier). Lindsay et al. (1976) established the presense of asymmetric labyrinth reflexes and in describing the pattern of interactions with neck reflexes it was concluded that neck and labyrinth should be considered as a single system important in the control of posture with the labyrinth and neck acting together to provide stabilization of the trunk.

Although Lindsay et al. (1976) confirmed that the reflex output with lateral head tilts sums to zero, their experiments cannot distinguish between the two models of labyrinth and neck interaction (von Holst and Mittlestaedt, 1950, and Roberts, 1967), since the underlying mechanism behind the labyrinth reflex is dependant upon the response charateristics of otolith afferents and the subsequent neural circuitry involved.

Since the early work on otolith function there has been considerable literature detailing the response dynamics of otolith afferents, and of cells located in the central nervous system receiving otolith input.

As described by Lowenstein and Roberts (1950) otolith afferents respond in a maintained fashion to static head tilts. All such units described by Lowenstein and Roberts show increased discharge with side-up tilts. In studies on otolith afferents in cats (Vidal, Jeannerod, Lifschitz, Rosenberg & Segundo, 1971; Loe, Tomoko & Werner, 1973) and in squirrel monkeys (Fernandez, Goldberg & Abend,

1972; Fernandez and Goldberg, 1976a & b) it has been shown that afferents exhibit greatest sensitivity to tilts about specific vectors. These vectors correspond to the morphological axis of polarisation of the hair cells supplied by the afferents. The polarisation vector is defined as the axis running from the smallest stereocilium to the kinocilium of an individual hair cell. In the utricle these vectors lie in a near horizontal plane whereas in the saccule they lie in a saggital plane. Consequently utricular units of the type described by Lowenstein and Roberts (1950) are common, but the majority of units described by others (Vidal et al. 1971; Goldberg and Fernandez, 1975) show response characteristics opposite to this. A ratio of aproximately 3 to 1 of utricular units who display increased tonic firing on side-down tilts are consistently observed. Units of utricular origin are therefore most sensitive to lateral tilts around the normal position with the majority of cells being excited by side-down tilts or contralaterally directed linear accelerations. Many units also show a dynamic component in their response to tilting (Vidal et al. 1971; Goldberg and Fernandez, 1975; Fernandez et al. 1972). This phasic component may then be partly responsible for the generation of phasic or phasic/tonic reflexes as described by Lindsay (1975).

The prevalence of ipsilateral excitation in populations of utricular afferents is also reflected within their projections to the vestibular nuclei. Single unit studies of Deiters nucleus (lateral vestibular nucleus)

which receives a large projection from the utricle (Brodal, Pompeiano & Wallberg, 1962; Gaeck, 1969), have revealed, using natural vestibular stimulation, units showing an increase in discharge with side-down tilts and a decreased discharge with side-up tilts. Units showing behaviour reciprocal to this were also described. These responsive units were termed alpha and beta respectively by Duensing and Schaefer (1959). In a study on the activity of lateral vestibular nuclear cells in response to lateral changes in head position Fujita, Rosenberg and Segundo, (1968) reported that 66% of responsive units displayed alpha like characteristics. The remaining 33% were beta like. From the results of Peterson (1970) the ratio of alpha:beta responses within the lateral vestibular nucleus is found to be close to 3 to 1. On this basis, and on information concerning the facilitatory influence on limb motoneurones from vestibulospinal tract stimulation (Lund and Pompeiano, 1968 and Maeda, Maunz & Wilson, 1975), an ipsilateral pathway of labyrinthine reflexes was favoured above a contralateral one. Roberts (1978) second edition of his book differs from the first in that the model of Lowenstein and Roberts (1950) is not discussed with respect to pathways, the reflex behaviour of the muscles only are considered.

In a recent study on the behaviour of central vestibular neurones Schor, Miller and Tomoko (1984) describe the distribution of direction vectors within the lateral vestibular nuclei of decerebrate cats. By tilting the head slowly in combinations of directions, the

direction producing maximal rate of firing increase could be predicted by vectorial addition. This was done in cats in which the semicircular canals were rendered non-functional. The results from 100 cells therefore reflect the behaviour of neurones receiving otolith projections. For each cell a particular vector of maximal sensitivity in the horizontal plane was established. Of the 100 cells there was no uniform distribution of vectors. Particularly noticeable in this study was the absence of cells responsive to tilts in the fore and aft directions. This is in agreement with the results of Adrian (1943), and Fujita et al. (1968). Interestingly, cells with vectors indicative of excitation with side-up tilts (beta response) were statistically demonstrated to be more sensitive to tilt than cells showing an increase in firing on side-down tilts (alpha response). The number of cells displaying alpha like responses equalled 66%, the remaining 34% showing beta like behaviour (as found by Fujita et al. 1968). Of these cells those excited by side-up tilts tended to be located ventrally in the lateral vestibular nuclei, while those excited by side-down tilts were more evenly distributed throughout the nucleus (cf. Schor and Miller 1982). This distribution of cells within this nucleus may be important, as a somatotopic representation prevails in the vestibular nuclei.

The lateral vestibular nuclei receives a non-uniform distribution of afferent projections from the labyrinth (Brodal et al., 1962) the majority of monosynaptic terminations being located ventrally.

Furthermore in respect to spinal projections the nuclei can be divided into forelimb (rostroventral) and hindlimb (dorsocaudal) regions. Based on this information it may be that the beta like cells show a higher sensitivity as a consequence of stronger, more direct synaptic linkage with the labyrinth. The results of Schor et al. (1984) demonstrate that despite a broad distribution of responsive units to a variety of head tilts the lateral vestibular nuclei may be specialized in the control of muscle groups that influence side to side stability, and, not fore and aft stability. The lateral vestibular nuclei must therefore be considered as a favourable site for relaying the asymmetric reflexes described by Lindsay et al. (1976).

In studies on otolith reflexes Schor and Miller (1981, 1982) characterised the dynamic responses of both neck and forelimb extensor muscles during sinusoidal roll tilt in decerebrate cats. By studying forelimb reflexes in normal cats and in cats with all six semicircular canals plugged (Schor & Miller 1981), the otolith contribution to vestibulospinal reflexes in an extensor muscle of the forelimb was assesed by recording EMG during sinusoidal rotation (0.01 to 2Hz). With low frequency of rotation the response in both groups of cats was essentially similar. The pattern of reflex activity agreeing with the results of Lindsay et al. (1976), in that compensatory activity increases in extensor activity accompanying side-down tilts. For frequencies below 0.1Hz both normal and canal plugged cats possesed flat gain and phase characteristics. But on sinusoidal tilts above 0.1Hz a considerable phase

lag with respect to position develops (approximately 180 degrees) in canal plugged preparations as opposed to a slight lead in cats with functioning canals. These results indicate that the otolith organs are responsible for the low frequency response of forelimb extensors but with higher frequencies of tilt an additional input from the semicircular canals serves to maintain a compensatory reflex. Compensatory reflexes from the otoliths are therefore only effective independently of the semicircular canals during static tilts or slowly modulated position changes.

In a follow up study, Schor and Miller (1982) compared the dynamics of central vestibular neurones with the dynamics of the muscular activity induced in neck and forelimb extensors by sinusoidal tilt. Although other workers have characterised the dynamics of vestibular neurones to sinusoidal tilt (Boyle and Pompieano, 1980), this work was carried out on canal plugged preparations, and is therefore specifically concerned with otolith reflexes. Neurones within the vestibular nuclear complex were identified by antidromic stimulation as belonging to one of the vestibulospinal tracts. By correlating the behaviour of vestibular units to the dynamic behaviour of the muscles the following results were obtained.

As described above forelimb extensor muscles develop a progressive phase lag at frequencies of sinusoidal tilt above 0.1Hz in canal plugged cats. Of the neurones which exhibited similar phase characteristics to the muscles the majority displayed beta-like responses,

with only one out of 55 alpha units behaving with phase characteristics similar to muscle (39 out of 48 beta cells showed muscle-like phase relations). The majority of these cells contributed to the various vestibulospinal tracts. Of the beta like cells showing muscle like phase characteristics 80% projected to the spinal cord. If these cells play a part in vestibulospinal reflexes, and the pathway to extensor motoneurone is facilitatory, then they must be involved in a pathway which projects to the contralateral motorneurone pools. The alpha-like cells which show flat phase relations can theoretically contribute towards otolith reflexes at low frequencies of tilt, though one would imagine that these cells acted ipsilaterally. The dynamic behaviour of triceps during sinusoidal rotation is proposed to result from a participation of ipsilateral alpha and contralateral beta neurones at low frequencies. The phase lagging behaviour of the muscle at frequencies greater than 0.1Hz indicates that only the beta neurones are appropriate for the observed reflex activity. The suggestion of a contribution from the otoliths to the contralateral reflex supports the predictions of Lowenstein and Roberts (1950). Schor and Miller's (1982) experiments are, however, only indicative, but are to some extent supported by results achieved by electrical stimulation of the whole labyrinth in decerebrate animals (Maeda et al. 1975).

[Whole labyrinth stimulation generates a non-specific increased discharge in afferents responding to otolith and canal inputs, consequently, activating both

alpha and beta type vestibular units, as well as those receiving convergent canal inputs. Maeda et el. (1975) reported that whole labyrinth stimulation results in excitatory synaptic potentials bilaterally in forelimb extensor motoneurones. This demonstrates that a pathway to the contralateral motor pool exists, although little else of functional significance can be attributed to this due to the non specific stimuli.]

By studying the effect of vestibulospinal tract lesions on roll tilt reflexes Miller, Roosin and Schor (1982) reported that lesions to the medial vestibulospinal tract did not significantly alter the reflex behaviour of either neck or forelimb muscles. Unilateral section of the lateral vestibulospinal tract at C2-C3, however had marked effects on the reflex behaviour of the contralateral triceps. It should be noted that these lesions also involve ipsilateral reticulospinal tracts either wholly or partially. The reflex behaviour of triceps ipsilateral to the lesion approached normal. The reflex response of the contralateral triceps was however reversed at low frequencies of sinusoidal tilt. At tilt frequencies greater than 0.1Hz the phase characteristics of the contralateral triceps approached normal values. However, at these frequencies of tilt a semicircular canal component becomes important in forelimb vestibulospinal reflexes (Schor and Miller, 1981). The apparent normal behaviour of both ipsi- and contralateral triceps at these higher tilt frequencies indicates that both crossed and uncrossed canal-forelimb pathways operate and, since the reflex responses of the

muscles are asymmetric the drive or the sign of these pathways is different.

The reflex reversal seen in triceps on the side opposite to the lesion during low frequencies of tilt is analogous to the reflex reversal seen in acutely hemilabyrinthectomized cats by both Nagaki (1967) and by Lindsay and Rosenberg (1978) following static head tilts. In these experiments the tonic labyrinth reflex on the side of the lesion is unaltered (i.e., side-down tilts lead to extensor facilitation), but the response of the contralateral extensor (on the side of the intact labyrinth) is reversed. A side-down tilt, with respect to the side of the lesion, results in a reduction in extensor tone. The pattern of reflex behaviour in the hemilabyrinthectomized cat is one of symmetry between the limbs. As in the tonic reflex, the reflex behaviour of muscles during low frequency sinusoidal tilt results from the activation of the otolith organs. In the experiments of Miller et al. (1982) the phase behaviour of triceps ipsilateral to the lesion was normal but, as mentioned previously the phase of the reflex response in the opposite triceps was reversed. The reversal in the direction of the otolith reflex on the intact side in both hemilabyrinthectomized (Nagaki, 1967; Lindsay and Rosenberg, 1978), and in spinal lesion experiments (Miller et al., 1982) suggests that in intact cats the ipsilateral otolith influence is inappropriate to provide the necessary compensatory reflex. The interruption of the ipsilateral pathways by spinal lesions does not affect the nature of

the reflex on the side of the lesion. This suggests that for the normal appearence of the otolith reflex, a crossed pathway has to operate. A crossed otolith-spinal pathway might therefore be utilized as a relay within the vestibular nuclei for the information signalled to the beta cells, which as described by Schor and Miller (1982) show muscle like phase relations to sinusoidal tilt. In this study of the response characteristics of vestibular neurones Schor and Miller (1982) suggested that the beta units could contribute toward a contralateral otoilth forelimb reflex with the alpha units possibly influencing the behaviour of ipsilateral extensor muscles at low frequencies of sinusoidal tilt. An influence from the alpha units on extensor muscles during these otolith reflexes seems unlikely in light of the results from experiments performed on cats with spinal lesions, and from cats following acute hemilabyrinthectomy. If a facilitatory drive to motoneurones from the ipsilateral alpha vestibular units operated, it would be expected that by removing the crossed pathway the reflex would still operate in the same direction (i.e., side-down tilt increasing extensor tone). This, however, is not the case. The reflex on the intact side, deprived of a contralateral influence shows a reversal in the response to tilt (a side-down tilt producing relaxation of the extensor). It would therefore appear that in this case a beta response has been imposed ipsilaterally on the muscle. Both crossed and uncrossed otolith-spinal reflex pathways would appear to exist, and utilise in some, as yet unknown, manner the behaviour of

the beta vestibular neurones. In the intact cat with two functional labyrinths the production of an asymmetric form of compensatory reflexes, resulting from static or slowly modulated head tilts requires that the crossed otolith pathway exerts a more powerful influence upon extensor motoneurones than that arising from the ipsilateral otolith. With more rapid head tilts a canal influence is recognised in the behaviour of the muscles (Schor and Miller, 1981), this influence is unchanged following spinal lesions indicating that both crossed and uncrossed canal-spinal pathways probably cooperate in the production of compensatory reflexes to movements of the head.

In this scheme of reflex connectivity otolith and canal influences are transmitted to muscles of the opposite side by first descending in the ipsilateral half of the spinal cord prior to crossing over. Such a pathway was described by Maeda et al. (1975) from studies using elsctrical stimulation of the labyrinth. From the results of Miller et al. (1982) it therefore appears that alpha vestibular neurones do not seem to play a role in otolith reflexes. In this respect the authors suggest that these cells serve to provide a static level of background facilitation to extensor motoneurones. If true, this would explain why 8th nerve section or lesions to the lateral vestibulospinal tract result in a loss of extensor tone ipsilateral to the lesion. The tilt modulation of these units, however, makes it unlikely that this is the sole function of these spinal projecting neurones.

The pattern of proposed pathways suggested by Schor

and Miller (1982) has close similarities to the original scheme of pathways presented by Lowenstein and Roberts (1950), in that otolith reflexes are seen to be predominately contralateral, and the adequate stimulus appears to operate through cells that show increased firing with side-up tilts.

Although the experiments of Miller et al. (1982) are chiefly concerned with lesions to vestibulospinal systems, the conclusion cannot be reached that these are the spinal tracts involved in the labyrinth reflexes. As mentioned previously all of these experiments involved in addition to a vestibulospinal lesion a non-specific lesion of reticulospinal tracts (a point stated by Miller et al., 1982).

Electrical stimulation of the labyrinth or the vestibular nerve is known to influence reticulospinal neurones located in the medullary and pontine reticular formation (Peterson & Felpel, 1971; Peterson, Filion, Felpel & Adzug, 1975; Peterson, Fukusima, Hirai, Schor & Wilson, 1980) as does vestibular nerve stimulation (Peterson and Adzug 1975). It has therefore been suggested that the reticulospinal system plays a part in the production of labyrinth reflexes. Natural stimulation of reticulospinal neurones has also been demonstrated to occur from the labyrinth (Manzoni, Pompeiano, Stampacchia & Srivastava, 1983). Manzoni et al. (1983) reported that out of the responsive reticular units identified as projecting to the spinal cord 58% showed an increased discharge with side-up tilts (beta-like response) and of the remainder,

33% displayed the opposite response (alpha-like), with 9% of cells showing intermediate characteristics. Of these cells the beta-like units show higher mean gain and sensitivity than is seen in units excited by side-down tilts. (The gain differences are reported to be significantly different, whereas the sensitivity differences are not compared statistically.) Interestingly, among these responsive units a higher proportion of cells excited by side-up tilt were located in more caudal regions of the reticular formation than in intermediate or rostral regions. In contrast cells showing increased output on side-down tilts were present in greatest density within rostral levels. This suggests that a somatotopic representation of tilt sensitive neurones may exist within specific reticular regions (Manzoni et al. 1983). The above responses result from the adequate stimulation of otolith receptors during slow sinusoidal tilts. With increasing frequency of tilts two populations of reticulospinal neurones can be identified. In one group as the frequency of stimulation increased above the threshold for canal related vestibular nuclear responses, no modification of gain or phase occurred, while in the other population a frequency response involving increased gain and phase was observed. In the first population it would appear that selective inputs from the utricle are involved, while in the second population convergence of otolith and canal inputs appears to occur. The results concerning the make up of these two sub-population of reticular units do not indicate whether a difference in the behaviour of alpha and

beta like units was noticeable.

Assuming that this study reflects a genuine representation of the distribution and behaviour of reticulospinal cells responsive to labyrinthine inputs, it is interesting to note that the proportions of alpha- to beta-like units is the reciprocal to that seen within the vestibular nerve and vestibular nuclei. This reciprocity of the relationship within the lateral vestibular nuclei and the reticular formation is taken by Manzoni et al. (1983) to reflect an otolith component from one side affecting the reticular formation of the opposite side. A direct ipsilateral and contralateral influence from the vestibular nuclei to the reticular formation has been demonstrated to exist (Ladpli & Brodal, 1968; Peterson & Adzug, 1975), although relays via the cerebellar nuclei may also take part. (The precise details of both ipsilateral and crossed pathways are unknown.) Despite a lack of knowledge of these pathways a topographic representation of tilt sensitive cells is evident within the reticular formation. It would appear that otolith signals related to different polarization vectors exert selective control over portions of the medullary reticular formation. The majority of these position sensitive reticulospinal tract cells are located in regions contributing mainly to the inhibitory lateral reticulospinal tract. From these observations Manzoni et al. (1983) conclude that during tilt in one direction a facilitation of extensor tone results, on that side, as a result of an ipsilateral excitatory influence from vestibulospinal systems, and also from a disinhibition from

recticulospinal systems. From a functional viewpoint the modulation of inhibitory reticulospinal tract cells by head tilt must, at a spinal level, cooperate with the proposed vestibulospinal relations to produce asymmetric reflexes. The outcome of this cooperation following hemilabyrinthectomy or spinal lesion requires that the efficacy of ipsilateral reticulospinal relations is less strong than the proposed ipsilateral beta vestibulospinal relationship. This would then allow reflex reversal on the intact side.

Although the presence of the above pathways has been demonstrated, it remains an open question of whether they actually participate in naturally evoked labyrinth reflexes. The responses of both reticular and vestibular neurones projecting to the cord make it likely that both systems operate in the production of labyrinthine reflexes. In discussion of these pathways it has been generally assumed that the activity of cells within spinal projecting regions of the reticular and vestibular nuclei reflect the behaviour of the extensor motorneurones demonstrated to participate in labyrinth reflexes. Both vestibulospinal and reticulospinal tracts have been demonstrated to influence either directly or indirectly different species of motoneurone. Similarly the action of labyrinth reflexes, although well characterised for forelimb extensors, is likely to involve other limb muscle groups. Clearly more experimentation is required in order to resolve the pathways involved in otolith reflexes, and also to characterise the behaviour of other muscle groups that may

be involved.

The activity of cells projecting to the spinal cord can be strongly influenced by the cerebellum. Labyrinth reflexes are also under influence from the cerebellum. Like hemilabyrinthectomy and spinal lesions, cerebellectomy leads to profound changes in the pattern of tonic labyrinth reflexes. Following cerebellectomy Lindsay and Rosenberg (1977) and Dutia, Lindsay and Rosenberg (1981) demonstrated that head tilts to the left or to the right led to simultaneous contractions in triceps of both forelimbs. Each limb showing contraction with side-up and side-down tilts. The mechanism behind this observation is not well understood, but what is apparent is that the cerebellum is necessary for the development of appropriate compensatory reflexes (Lindsay and Rosenberg, 1977; Dutia et al., 1981).

Both primary and secondary vestibular projections to the cerebellum exist, and the vestibular nuclei have been shown to receive direct connections from both the cerebellar cortex and nuclei. This demonstrates the intimate relation between the vestibular system and the cerebellum. Projections onto cells in the cerebellar cortex and nuclei serve as sites where integration between vestibular and other proprioceptive inputs can occur. For example, interactions between labyrinth and neck afferent activity. Both a climbing fibre and a mossy fibre projection from neck afferents has been demonstrated (Wilson, Maeda & Franck, 1975a, b; Wilson, Maeda, Franck & Shimazu, 1976). The floculus receiving an afferent projection from receptors located in the neck (electrical

stimulation of the C2 ganglion) and relaying within Brodal and Pompeiano's group x.

Natural stimulation of neck afferents has also been demonstrated to influence the behaviour of Purkinje cells of the cerebellar vermis (Denoth, Magherini, Pompeiano & Stanojevic, 1979, 1980). Recording from Purkinje cells during sinusoidal neck and whole body rotations it was found that the majority of responsive cells showed an increase in discharge on side-down tilts of the neck (the phase of the response suggests a position sensitivity or dependence). The effects of neck rotation were opposite to those seen when whole body tilts were employed. Side-down tilt of the whole animal led to a decrease in the discharge rate of Purkinje cells, side-up tilt producing excitation. When labyrinth and neck stimulation were simultaneously evoked units showing otolith and neck convergence displayed a residual signal that was related to the neck signal. From this it would appear that an incomplete interaction of labyrinth and neck afferences occurs within the cerebellum.

The neck afferent input to the cerebellar vermis seems unlikely to result from the pathway relaying via group x as described by Wilson et al. (1976), since the effect described dy Denoth et al. (1980). can be mediated through the precerebellar lateral reticular nucleus whose neurones are also excited during side-down rotation of the neck (Kubin, Manzoni & Pompeiano, 1981).

As described earlier Roberts (1973) and others (Lindsay et al. 1976; von Holst & Mittlestaedt, 1950) have

proposed that interactions between antagonistic otolith and neck reflexes allow an animal to make voluntary head movements without reflex constraint. The results just described illustrate only one possible site for this interaction. The interaction seen by Denoth et al. (1979) although not complete can however be considered as a component step in the integration of both labyrinth and neck reflexes.

In recent years several sites of integration of labyrinth and neck reflexes have been studied. These include the vestibular nuclei and spinal interneurones. The vestibular nuclei have long been recognised as an important site in the integration of ascending spinal influences (Wilson, Kato, Thomas & Peterson, 1966; ten Bruggencate, Teichmann & Weller, 1972a,b,c, 1975 a,b). In a study on the convergence of vestibular and somatic influences of the vestibular nuclei Fredrickson, Schwartz & Kornhuber (1966) noted that of the somatic influences converging on the vestibular nuclei the majority of responses were joint mediated. The magnitude of responses to changes in elbow or knee joint position appear equally strong as responses to neck torsion. Extension of the ipsilateral limb excited the majority of units studied, flexion inhibited these cells. Units responsive to neck torsion generally showed increased output on ipsilateral (side-down) torsion. Unfortunately cathodal and anodal stimulation of the labyrinths was used and not natural stimulation of the labyrinths. The use of non-specific electrical stimulation precludes a full assessment of the interactions between vestibular and

somatic afferents from a functional viewpoint. The demonstration of modulation of the discharge of vestibular nuclei cells by changes in limb position allows the possibility that limb position is monitored by the vestibular system, acting either to condition vestibular reflexes or to act as a feedback from the limbs during excecution of vestibular reflexes. In a later study Rubin, Liedgren, Milne, Young & Fredrickson (1977) re-examined the influence of joint position on vestibular nuclear cells. Interestingly of the units Rubin et al. (1977) described as sensitive to limb position the majority were located in the lateral vestibular nuclei. It would therefore appear that input from the joints (both limb and neck) play a role in supplying postural information to the vestibular nuclei and in particular to regions involved in tonic reflexes. (Evidence exists that Ia muscle afferents do not contribute in position signalling to the vestibular nuclei, Pompeiano and Barnes, (1971)).

In a study principally concerned with the effects of natural neck stimulation on vestibulospinal cells Kasper and Thoden (1981) reported that of an identified 151 spinal projecting vestibular cells only 16 (10.6%) showed modulation with neck stimulation. Furthermore only 3 were influnenced by both vestibular and neck inputs. A possible explanation of the small number of responsive cells observed may have been due to the method of neck stimulation. Lateral bending of the cervical column was used as a neck stimulus. As neck reflexes take origin mainly from receptors from the upper three cervical

vertebra it would seem that such a stimulus is in-appropriate in light of the anatomical arrangement of the atlas and axis. The atlas and axis are specifically modified to allow rotations of the head upon the neck and therefore rotational stimuli would appear to be a more natural form of stimulation of receptors located around these vertebra.

In a study investigating rotational neck influences on vestibulospinal neurones Boyle and Pompeiano (1980) reported that of a population of identified vestibulospinal neurones almost 66% showed a response to neck rotation. The phase of the response to neck rotation was observed to be related with neck position, with almost equal representation of cells showing increased or decreased neuronal activity on side-down rotations. Such a representation of neck input to the lateral vestibular nuclei suggests that the vestibular system may participate in neck reflexes. A scheme suggestive of a pathway involving the cerebellum has been proposed by Boyle and Pompeiano (1980). The authors suggest that inhibition from Purkinje cells of the cerebellar vermis (which also show increased discharge on side-down neck rotations Denoth et al. (1980)) act on vestibulospinal neurones which in turn influence the behaviour of motoneurones. Although theoretically possible, this scheme is not the only way neck afferents can influence these vestibulospinal neurones. Neck responses have also been recorded in reticular regions (Kubin et al., 1981) known from anatomical studies to project directly to the lateral

vestibular nuclei as well as to the cerebellum. In addition neck reflexes are unaltered following spinalization (Magnus, 1926), thereby demonstrating that a spinal pathway can operate without the need for higher centres being involved. The neck reflex pathway would appear to be very poorly understood, a possible explanation for this is perhaps the uncertainty over what receptors, and hence afferents contribute to the reflex.

In a companion study Boyle and Pompeiano (1981) looked at the interactions between neck and macular inputs onto vestibulospinal neurones. Out of the total population of cells examined 48.7% (75/154) responded to both macular and neck inputs. Interestingly a higher proportion of cells were found in rostroventral regions of Deiters nucleus, an area known to project to cervical segments of the spinal cord. Most of the units receiving convergence from both types of receptors showed reciprocal responses to the two inputs, the predominant pattern of responses was excitation during side-up tilt of the neck and inhibition following side-up tilt of the whole body. A proportion of units showed a synergistic parallel convergence of inputs, these cells were excited during both side-up neck and body tilts. Of the units displaying convergence their output corresponded to the vectorial summation of the individual responses. This then requires that for a cell to display no alteration in activity during joint labyrinth and neck stimulation the two inputs must oppose each other exactly. The results of Boyle and Pompeiano (1981) suggest that within the rostroventral portion of Deiters nucleus the

labyrinth has relatively greater influence on cells showing convergence while in dorsocaudal regions the neck influence is the strongest. The behaviour of these cells during combinations of vestibular and neck inputs demonstrates that the neck can modify the activity of cells in the vestibular nuclei that project to cervical and lumbosacral regions of the cord. On the information available it would therefore appear that a stronger labyrinth input is relayed to the forelimbs and a stronger neck input to the hindlimbs. From a functional consideration of the interactions between labyrinth and neck reflexes it is apparent that for a net zero alteration in reflex output to the limbs a further integration of neck and labyrinth afferences has to occur. The possibility of interactions at an interneuronal level has been studied by Wilson, Ezure & Timerick (1984).

The dynamics of both otolith (Schor & Miller 1981) and neck reflexes (Ezure & Wilson, 1983) in forelimb extensors are consistent with observed interactions between these reflexes on rotation of the head (Roberts, 1973, 1978; Lindsay et al., 1976). In a study investigating this interaction Wilson et al. (1984) described the dynamics of spinal interneurones showing responses to natural neck afferent stimulation, and also its interaction with an otolith signal was also studied. Interneurones located within lamina 7 and 8 were recorded from during sinusoidal neck stimulation. The responses of 115 neurones modulated by neck rotation were analysed. Sixty two of these neurones were recorded from labyrinthless cats, the remaining 53

were recorded from cats with intact labyrinths. Out of this population of cells, 56 were excited by side-up rotation (termed type I response) and 59 were excited by side-down rotation (termed type II response). The behaviour of cells from cats without labyrinths was similar to that seen in cats with labyrinths. The dynamic behaviour of type I and type II cells was the same. At low frequencies of tilt the response followed neck position. The response of type I cells is in phase with the activity of ipsilateral triceps during naturally evoked neck reflexes, while that of type II cells is 180 degrees out of phase with ipsilateral extensor activity.

In cats with intact labyrinths a subpopulation of neurones were tested for neck-vestibular convergence. From a total population of 40 tested neurones, 21 cells were classified as receiving an otolith input (responding with a phase closely related to head position at low frequencies of tilt < 0.5Hz). Within this group of 21 cells, 8 displayed alpha responses (increasing discharge with side-down tilt), while the 13 remaining cells showed beta like responses (increased discharge with side-up tilts). Importantly, of the 8 alpha-like and 21 beta-like cells, the neck response of each cell was seen to be antagonistic. In other words type I neck interneurones receive alpha-like otolith convergence and type II neck interneurones receive a beta pattern of otolith convergence. This pattern of convergence seems therefore to reflect the pattern of interactions within forelimb muscles on simultaneous otolith and neck stimulation. It is tempting to conclude

that these interneurones are part of a common link to motoneurones within both neck and otolith reflexes. In this respect it would therefore be significant that there appears to be a greater number of cells showing beta to type II convergence than alpha to type I convergence. Although the majority of the cells recorded from are located in areas known to contain segmental or propriospinal neurones that project to forelimb motoneurones, there is no direct evidence that the cells seen by Wilson et al. (1984) relay information to motonerones. It is also possible that these cells may be spinoreticular neurones projecting to the lateral reticular nucleus, an area known to show responses to both labyrinth and neck inputs (Kubin et al., 1981). As little is known about the projections or inputs of these interneurones one cannot distinguish between the above possibilities.

The results from Wilson et al. (1984) highlight one of the major problems concerning the assignment of a functional role to groups of cells showing responses to either or both labyrinth and neck proprioceptive input. Due to an incomplete understanding of muscle groups participating in both labyrinth and neck reflexes single unit studies have discussed their results with reference to the well documented pattern of reflex activity demonstrated to occur in triceps. As mentioned earlier, however, several authors using natural stimulation techniques have described responses in flexor musculature (Beritoff, 1914; Tait & McNally 1925a; Rademaker, 1935). Although the evidence surrounding the involvement of limb flexors in labyrinth

and neck reflexes is contradictory, it is evident that a descending input to muscle groups other than the extensors cannot be ruled out. Experiments utilizing electrical stimulation of the vestibular nerve (Maeda et al., 1975; Maeda, Magherini & Precht, 1977) or individual ampullary nerves (Suzuki & Cohen, 1964) have shown that pathways to flexor motoneurones exist. In consequence, the lack of understanding concerning the reflex output at the motoneuronal level, and of the relationship between different muscle groups make it difficult to index the response patterns of cells within proposed pathways to a functional role. Similarly, shortcomings within our understanding of the muscle fields controlled by cells projecting from the vestibular nuclei, reticular formation and of proposed propriospinal interneurones make it difficult to identify the complete reflex pathways. One of the aims of this thesis is to determine what relationships exist between various forelimb muscle groups during naturally evoked labyrinth and neck reflexes.

CHAPTER 2. Methods

2.1.0. Introduction.

The format for this section of the thesis is as follows. There are three main headings which are further subdivided into smaller individual components. The main title headings cover the following (1) Animal preparation, (2) stimulation techniques, and (3) data handling and recording techniques. As experiments have been performed on cats with intact labyrinths, acute and chronic hemilabyrinthectomized cats, and cats with bilateral labyrinthectomy the animal preparation section will deal with each surgical procedure separately. The protocol for each type of preparation being a selection of the individual procedures and will be summarised at the end of the section.

ANIMAL PREPARATION

2.1.1 Anaesthesia.

All the experiments to be described were carried out on adult cats weighing from 1.8Kg to 3.0Kg. All animals were deeply anaesthetized prior to, and during any surgical procedure. Anaesthetic was induced by allowing the animal to breath a gas mixture of N_2O(80%) and O_2 (20%) plus Halothane. The cats were judged to be anaesthetized on the disappearence of withdrawal reflexes in the limbs and of

corneal reflexes on touching the eye.

2.1.2 Decerebration.

In preparing the animal for decerebration a tracheostomy was performed and the common carotid arteries either permanantly or temporarily ligated. The tracheostomy was performed in order to facilitate the removal of any mucus build up during the course of an experiment, while the carotid ligation resulted in a reduced blood loss during the actual process of decerebration. Following tracheostomy, the cat's body was supported in a prone position with the head securely held by fixation in a Roberts' head holder (Roberts, 1951). The technique employed in decerebration was essentially the classical method described by Sherrington (1898). With the cat in the above position the skin on the back of the head is shaved and cleared of loose hairs. A midline incision is made along the top of the head and the skin is retracted to expose the right temporal muscle. This muscle is then separated from the underlying bone and removed. A hole is trephined in the parietal bone of the right side and radially enlarged using bone forceps to a diameter of about 2cm. The edges of this hole are sealed firstly with bone wax, and then smeared with a small quantity of vaseline. This not only stops occasionally troublesome bleeding from the diploic veins but also reduces the risk of air embolism developing during the course of the experiment. With the dura covering the cortex now visualized, the vertebral

arteries are occluded by exerting pressure behind the transverse process of the atlas, successful occlusion results in a sinking of the dura. The dura was then opened and using a blunt spatula the occipital lobe of the cortex is either reflected or removed so that the colliculi can be seen. The spatula is then used to make a transverse section across the neuraxis. The cut is angled to slope forward,and is made either between the inferior and superior colliculi (intercollicular) or just anterior to the superior colliculi (precollicular). The cut is carried through to the base of the skull and all brain tissue above the section is removed from the skull cavity. Any resulting bleeding was controlled by exerting pressure on a pad of cotton wool placed over the base of the skull. The compression of the vertebral arteries was discontinued and the anaesthetic temporarily switched off. On releasing the vertebral arteries the blood supply to the brain stem is re-established after having been interfered with for only the one or two minutes taken for the decerebration to be completed. In some instances respiration ceased immediately after decerebration but spontaneous breathing always resumed following a short period of artificial respiration. Once sufficient time had elapsed to allow clotting to occur at the floor of the skull, the cavity was loosely packed with cotton wool. The cat was then left for several minutes, during which time rigidity was established in the limbs.

2.1.3 Denervation of atlanto-occipital and atlanto-axial

joints.

In order to achieve, in one preparation, independently evoked labyrinth and neck reflexes, using adequate stimulation, it is necessary to make the provision whereby head rotation does not produce activation of receptors involved in neck reflexes. This section details the surgical steps that allow this, the methods of stimulation will be described in a latter section. Isolation of labyrinth and neck reflexes is achieved in these experiments by the denervation of the atlanto-occipital (C1) and atlanto-axial (C2) joints. In order to achieve good experimental results this procedure must be carefully and extensively carried out. To gain access to the first and second cervical nerves both gross and fine dissection is required. Prior to the onset of surgery the administration of anaesthesia is resumed. Although the animals are decerebrate the anaesthetic removes any tendency for movement to occur during the dissection. The skin incision made prior to decerebration is extended caudally above the neck, allowing the superficial neck muscles to be visualized. The trapezius muscles originating from medial halves of the lamboidal crest and from the midline to the caudal end of the spinal process of the axis are cut free from their insertions onto the lamboidal crest and split medially. Once split the muscles can be retracted so as to gain access to the deeper muscles of the neck. Directly beneath the trapezius group of muscles lies splenius, this muscle which when activated

bilaterally elevates the head is treated in a similar fashion to trapezius. Lying on each side of the neck the left and right portions are carefully separated from their origins on the lamboidal ridge and are divided medially. Another muscle which must be cut bilaterally from its insertions on the lamboidal crest is the elevator, biventor cervicis. This muscle makes its origins along the spinous processes of cervical and thoracic vertebra and for the purposes of this dissection it is separated bilaterally to the level of the third cervical vertebra. On retraction of the above muscles the modified interspinales muscles which are associated with the dorsal aspects of the axis, atlas and the occipital region of the skull can be clearly seen. With the aid of a dissecting microscope the attachments of these muscles are cleared from the spinal process of the axis, and from the dorsal surfaces of the atlas and the supraoccipital region of the skull. It was suggested by McCouch et al. (1951) that neck reflexes can persist if the articular surfaces just mentioned are not carefully cleared of tissue. These authors suggesting that neck reflexes result from the activation of joint receptors whose nerves lie in the facsia covering the intervertebral foramena. Recent work however (Richmond and Bakker, 1982), has questioned this conclusion on the basis of an apparent lack of Ruffini endings in these regions. Despite this controversy the original result of McCouch et al. (1951) that neck reflexes are only abolished following procedures that would interrupt the hypothesized joint afferents make it essential in these experiments that the fascia and

ligaments covering the intervertebral foramena are treated as probable sites for the generation of neck reflexes.

In order to eliminate reflex effects from the C2 region, the fascia is cut circumferentially around the second cervical nerve, and the nerve roots sectioned proximal to the dorsal root ganglion. For convenience the ventral roots are sectioned along with the dorsal roots, this procedure is carried out bilaterally. To section the dorsal roots of C1 an intradural approach was employed. The dura was exposed by splitting the atlanto-occipital capsule longitudinally. In most cases a small area of the dorsal surface of the atlas was removed to facilitate access to the spinal cord. The dura was then cut near the dorsal root entry zones and by gently lifting it the dorsal root filaments can be seen joining the spinal cord. The rootlets can then be cut, this procedure was carried out bilaterally. The denervation of C1 and C2 allows naturally evoked labyrinth reflexes to be studied in isolation from neck reflexes by uncoupling the two reflex systems. Appendix A provides an illustrated guide to the above dissection.

2.1.4 Implantation of cuff electrodes round the superficial Radial nerve.

Cuff electrodes were implanted round the superficial radial nerves of the right and left forelimbs in order to investigate the modulation of electrically evoked flexion and crossed extension reflexes with

combinations of changes in head, neck, and elbow positions.

The superficial radial nerve is composed of two branches, the lateral and the medial branches. The nerve branches lie to each side of the cephalic vein which courses along the top of brachioradialis toward the forepaw. The nerve carries cutaneous afferents supplying the dorsum of the paw and the distal portions of the forearm. Careful dissection on a carcase also reveals a motor innervation to the lower portions of brachioradialis- electrical stimulation confirms this.

To implant the electrodes an incision of approximately 2cm is made slightly medial and parallel to the course of the nerve above brachioradialis. By lifting the skin with Spencer Wells forceps the lateral and medial branches can be seen lying in close proximation to the cephalic vein. By blunt dissection the nerves are freed from the surrounding fascia and a cuff electrode carefully placed round both branches of the nerve. The electrode is then stitched to the underlying muscle and the exposed portions of nerve coated with vaseline. The electrodes are constructed from chlorided silver wire inserted into short pieces of rigid plastic tubing. Viewed end on the tubing is 'C' shaped.

2.1.5 Labyrinthectomy.

As the effects of labyrinthectomy are investigated in acute and chronic preparations this section will deal with the method of destruction of the labyrinth. The

sections to follow will detail the special arrangements made for the welfare of the chronic cats.

The method of labyrinthectomy follows the procedure of de Kliejn (1912). This method employs a ventral approach through the bulla to gain access to the labyrinthine cavity. An outline of the surgical steps in the labyrinthectomy is given below.

The cat is anaesthetised as previously described (section 2.1.1) and placed in a supine position. By palpatation, the angle of the jaw is located and from this point moving slightly medial and caudally the position of the bulla is found. A skin incision is then made across this region starting from the angle of the jaw. On retracting the skin the large veins that unite to form the external jugular vein can be seen, as can the salivary glands that lie above the bulla. In approaching the bulla the mandibular gland is freed from the surrounding connective tissue and is displaced medially. The digastric muscle can then be seen and has to be both split and retracted in order to reach the bony surface of the bulla. At this point in the dissection great care must be taken as the external carotid passes superficially across the bulla. The artery is retracted caudally, and the wall of the bulla is perforated using a dental pick. The hole in the bulla is then enlarged with small bone forceps. At this point in the dissection, under suitable illumination, the round window can be partially seen. It is obscured to varying degrees by a bony partition which divides the middle ear into two parts. The bony wall is demolished and the fragments of

bone removed, so as to gain a full view of the inner ear. Using a dental probe or a small gouge the round window is opened and endolymph can be seen flowing from the inner ear. By rotating the probe between the fingers the labyrinthine cavity can be, to a large extent, evacuated.Remaining pieces of membranous labyrinth are removed with small forceps. The labyrinthectomy is complete when the bare bony wall of the auditory capsule is seen along with the the stump of the eighth nerve. During these final stages of the operation the internal auricular branch of the facial nerve should be visible and care should be taken so as to avoid damaging this nerve. On completion the bulla is packed with a small piece of cotton wool and the skin incision closed. This procedure is the same in both acute and chronic preparations and is carried out on the left labyrinth. In some instances a bilateral labyrinthectomy was carried out; these were acute experiments. The chronic experiments differ from the acute ones in one obvious respect, that is, they recover from the anaesthesia and undergo a period of recovery prior to the experiment, the acutes do not recover conseiousness.

2.1.6 Special provisions made for the post-op recovery of chronically hemilabyrinthectomized cats.

Hemilabyrinthectomy inflicts gross insult to the behaviour of any animal. For this reason great care was taken in management of the post-operative period and subsequent recovery phase of the selected animals.

Animals used in the series of chronic experiments were either specially purchased, on the basis of being free from infection, or were animal house stock declared infection free following administration of a course of antibiotics. In order to reduce the risk of re-infection from other animals, these cats were housed separately from the main cat stock.

Infection from any surgical intervention is likely if no special precautions are taken. For this reason labyrinthectomy in these animals was carried out under aseptic conditions in the operating theatre within the animal house complex. To further reduce the risk of infection the wound was liberally dressed with Acramide (Dales Pharmaceuticals Ltd). Acramide is a general purpose antibacterial dressing containing Aminacrine hydrochloride and sulphanilamide. These precautions resulted in all animals staying free of infection.

As recovery from gas anaesthesia is very rapid, it was decided that a post operative sedative should be administered to relieve this period of recovery where the effects of hemilabyrinthectomy are most profound. To this end, and in consultation with representatives of the University of Glasgow Vet School, a cocktail of two commercially available veterinary products was used. Injected intramuscularly, prior to the onset of gas anaesthesia, the cocktail contained a mixture of Rompun (Bayer) and Vetelar (Parke-Davis). Rompun's active ingredients include a sedative, an analgesic anaesthetic and a muscle relaxant while Vetalar contains ketamine. The

cats aroused very slowly from the action of this powerful sedation and exhibited no obvious signs of post operative pain. The individual cages were also fitted with red faced infra red heating lamps. These lamps helped to maintain a warm environment during the first days after the operation, the red faces minimise the disturbing effects caused by bright lights.

Food and water were made freely available to the cats on coming out of sedation and their weights were taken daily in order to judge their well being. After an initial weight loss, due to an apparent lack of appetite, all cats weights stabilized before increasing above pre operation levels. A daily diary of each cat's progress was made, this detailing the symptoms of the hemilabyrinthectomy and the condition of the animal. The cats were encouraged to move about and were frequently let loose in the laboratory for several hours at a time. This appeared to facilitate the recovery from the operation and allowed for a detailed survey of the resultant postural and locomotor disturbances and their reduction with time. The animals were catered for in this manner for at least eight weeks, whereupon they were put forward for experimentation.

2.1.7 Summary of surgical protocols.

In this section summaries of the protocols for the surgical preparation of animals forming the individual groups are given. The categories or headings that are considered are a) normal cats with intact labyrinths, b)

acute left labyrinthectomised cats, c) chronic left labyrinthectomised cats and d) bilaterally labyrinthectomised cats. Under each of these headings a list of the surgical steps in the preparation of the animal is given. These lists also give the relevant section numbers where detailed descriptions of the individual surgical steps can be found. The number of cats in each group is also given.

(a) Normal cat: intact labyrinths (31 cats)
anaesthetised - section 2.1.1
decerebration - section 2.1.2
C1 & C2 spinal nerves cut - section 2.1.3
implantation of cuff electrodes - section 2.1.4

(b) Acute hemilabyrinthectomy (26 cats)
anaesthetised - section 2.1.1
left labyrinthectomy - section 2.1.5
decerebration - section 2.1.2
C1 & C2 spinal nerves cut - section 2.1.3
implantation of cuff electrodes - section 2.1.4

(c) Chronic hemilabyrinthectomy (10 cats)
anaesthetised - section 2.1.1
left labyrinthectomy - section 2.1.5
period of recovery - section 2.1.6
anaethetised - section 2.1.1
decerebration - section 2.1.2
C1 & C2 spinal nerves cut - section 2.1.3

(d) Bilaterally labyrinthectomised cat (1 cat)

anaesthetised - section 2.1.1

left labyrinthectomy -section 2.1.5

right labyrinthectomy - section 2.1.5

decerebration - section 2.1.2

C1 & C2 spinal nerves cut - section 2.1.3

implantation of cuff electrodes - section 2.1.4

In all experiments anaesthesia was discontinued after completion of surgery. During the course of several experiments further surgical intervention was carried out. This could take the form of a T12 section or in normal cats, once the reflex behaviour of the animal had been established, a left labyrinthectomy was occasionally performed. Similarly a right labyrinthectomy was occasionally carried out in the course of experiments on both acute and chronic experiments. These occurrences will be detailed in the relevant results sections.

2.2.0 Details of animal fixation and stimulation techniques.

In this division of this chapter the details of the methods used in supporting and fixing the animal to the experimental apparatus and the methods used for stimulation of various receptors are given under appropriate headings.

2.2.1 Experimental apparatus and animal fixation.

Once surgery was completed the animal was transferred to the supporting frame. The apparatus used in support of experimental animals was originally designed by Dr T.D.M.Roberts and subsequently used by him and others in studies of labyrinth and neck reflexes. An integral part of this apparatus are facilities for the natural stimulation of the labyrinth and of neck reflex centres. The head, neck and trunk of the animal are independently supported. The weight of the trunk is supported by two knitting needles, one passing below the iliac crests the other through the supraspinous ligament of the upper thoracic vertebra. The knitting needles are secured by clamps to the supporting frame. The position of these supporting clamps can be adjusted so as to position the cat centrally with a straight back. The head is supported by a head holder (Roberts 1951) clamped so as to hold the head in an approximately normal attitude, the angle of the mouth lying 45 degrees to the horizontal. A clamp attached to the axis vertebra (exposed during surgery) supports the neck. Both the clamps supporting the head and the neck are integral parts associated with the methods of naturally stimulating the labyrinth and neck proprioceptors respectively. The details of the stimulation techniques follow in a latter section.

In the support of the forelimbs, steel pins were inserted into the humerus and ulna of both forelimbs. Brass rods were attached to the humeri pins and secured rigidly to the supporting frame so as to eliminate movements about

the shoulder. The lower arm was secured to a brass rod which could be rotated and held fixed at positions about an axis coincident with natural movements about the elbow. This allowed the position of the elbow to be changed during an experiment, further details of this are given in the section regarding joint receptor stimulation. The hind limbs were not rigidly fixed during the course of an experiment. Radiant heating lamps were attached to the supporting frame and maintained body temperature at 37+/- 1 degree centigrade, as monitored by rectal temperature.

2.2.2 Natural stimulation techniques (head, neck and joint).

As previously mentioned, natural stimulation is used to alter labyrinth and neck propriocetor output. The clamp supporting the head permitted head rotation about an anterior-posterior axis, whereas the clamp on the axis vertebra allowed rotation of the neck about an inclined axis passing through the vertebral column. Fig. 2 shows the axes of rotation about which head and neck movements are made. The position of intersection of these axes is critical to the success of an experiment. In positioning the cat in the frame a tissue clamp is attached to the the spinal process of the axis vertebra. By watching this clamp during head rotations it is possible to determine if the axis of head rotation is aligned correctly. Ideally, this axis of rotation should run along the midline and pass through the odontoid process of the axis vertebra. If

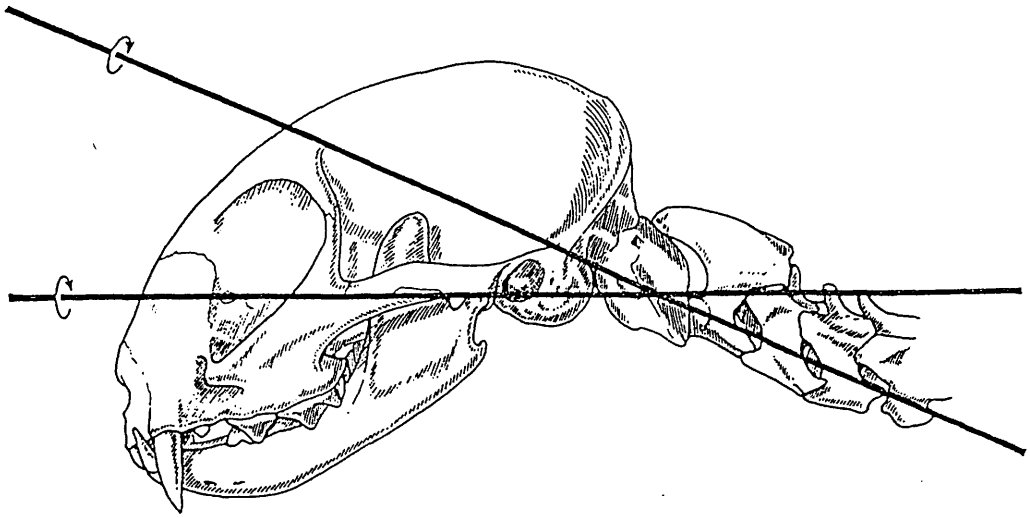


Figure 2. Diagram of cat skull and cervical spinal column, illustrating anterior-posterior axis of head rotation and the axis of neck rotation passing through the vertebral column. Note intersection of axes of rotation at odontoid process.

alignment is correct a head rotation should produce no movement of the clamp on the axis vertebra, if movement is seen, the position of clamps securing the head are altered until the desired result is attained. The tissue clamp is then replaced by the neck supporting clamp. This clamp is attached via a system of levers to a spindle about which rotations take place. These rotations being about an inclined axis passing through the odontoid process of the axis vertebra and the upper cervical column. The point of intersection of the axis of head rotation with the axis of neck rotation is the odontoid process (see Fig. 2). When the clamp on the axis is held fixed, a rotation of the head produces movement of the atlanto-axial and atlanto-occipital joints only. As these joints have been denervated no neck reflex responses develop and labyrinth reflexes can be studied in isolation from neck reflex contamination. Similarly neck reflexes can be studied in isolation when the head is held fixed and the clamp on the axis vertebra rotated. The resultant movements of cervical joints below the clamp produce neck reflex responses. Potentiometers were attached to the the spindles about which head and neck rotations took place. In this way head and neck position could be monitored. Head rotations are described as either to the right or to the left. A head rotation to the right indicates that the head is tilted laterally so that the vertex of the skull is rotated to the right side of the animal. Neck rotations will be described similarly, for example, a neck rotation to the left indicates that the spinous process of the axis vertebra is

rotated toward that side of the animal.

In the majority of experiments labyrinth and neck reflexes are produced in the manner just described. In several experiments on bilaterally labyrinthectomized cats, however, head rotations are used to elicit neck reflexes when C1 and C2 are intact. A head rotation to one side in these cats produces similar results to neck rotations in denervated cats. These preparations will be more fully described in the relevant results sections.

The main part of this thesis concerns the organisation of labyrinth and neck reflexes on different forelimb muscles in normal, acute and chronic hemilabyrinthectomized cats. Additionally, the effect of alterations in limb posture on labyrinth and neck reflex systems in these cats was studied. This was achieved by altering forelimb position by rotation about the elbow. This procedure has been shown to modulate the discharge of tonically active joint receptors (Baxendale and Ferrell, 1983).

The position of both elbows could be fixed at any position between 30 degrees and 165 degrees. In practice joint angles of less than 60 degrees were not used as considerable resistance to flexion is encountered beyond this angle. To test if limb position influenced labyrinth and neck reflexes joint positions representing flexed and extended postures were used as was a position midway between these two extreme positions. As described in the previous section bone pins were inserted into both humeri and ulnae. Attached to these pins were the devices used to

fix the forelimbs at different positions. Fig. 3 illustrates the components of these devices. Composed of two metal rods articulated about their common ends the metal rods could be rotated relative to each other about an axis passing through this articulation and fixed at the desired position. When this axis is aligned with the elbow joint, movement about it changes the position of the lower limb relative to the upper limb which is rigidly fixed to the frame. This movement about the elbow can be expected to result in changes in muscle length as well as altering joint receptor discharge. In order to differentiate between muscle and joint receptor actions intra-articular injections of a 2% lignocaine solution were given. This procedure is known to selectively abolish elbow joint afferent discharge (Baxendale and Ferrell, 1983) for up to one hour. This procedure allows a comparison to be made between results obtained at different joint angles before lignocaine injection with results gained following the injection. The contribution from various receptors to any reflex modulation observed can then be assessed.

2.2.3 Parameters of radial nerve stimulation.

Cuff electrodes placed around the superficial branch of the radial nerves were used to evoke, by electrical stimulation, ipsilateral and crossed reflexes. Electrical stimulation permitted an assessment of excitability in these reflex pathways by monitoring either reflex thresholds or the size of a reflex response to a

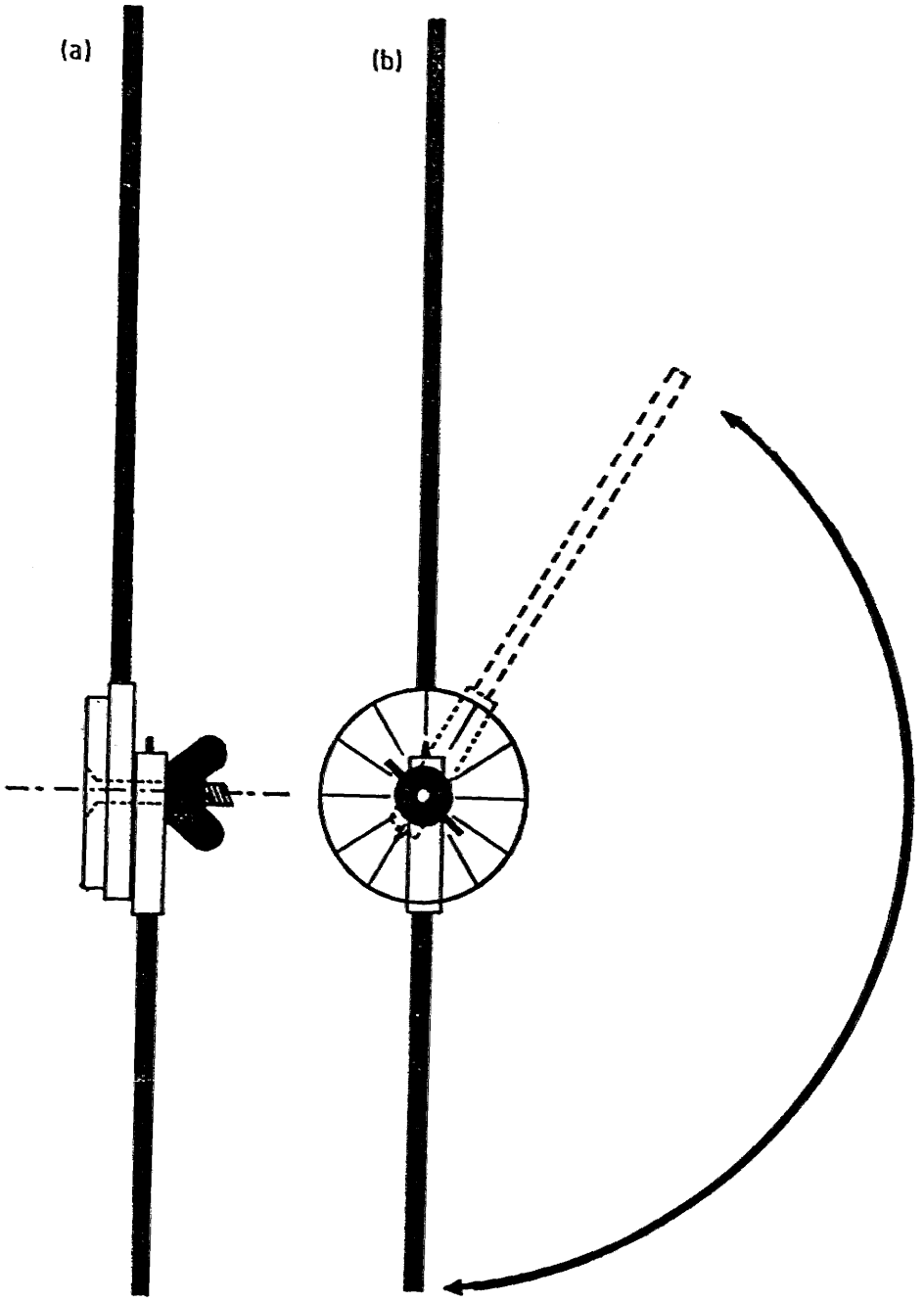


Figure 3. Diagram of apparatus used to fix the forelimb at different positions about the elbow. (a) side elevation, (b) frontal elevation. The humeris is fixed to the upper rods by steel pins and the ulna to the lower rod in a similar fashion. The lower rod can be fixed at any position within the arc defined in (b). The axis of rotation (passing through the wing nut) is positioned to coincide with the axis of rotation of the elbow.

fixed stimuli. Using a fixed stimuli as a test pulse it was possible to use alterations in head, neck and elbow position as conditioning influences on the resulting reflex response. In this way modulation of flexion and crossed extensor reflexes with changes in head, neck and elbow position could be assessed. This type of experiment was carried out in instances where the spontaneous activity of the decerebrate preparations fell to low levels, such that no direct consequences of alterations in head position were observable in the EMG of the muscle under study.

A choice of two type of stimulator were available for the generation of impulses, a Digitimer DS2 isolated stimulator or, from that companies Neurolog range a NL800 stimulus isolator (this stimulator is of the constant current type). For most experiments the DS2 stimulator was used as this was found to be more adaptable to the experimental situation. The stimulators were triggered from a Digitimer D4030. This instrument was programmed to deliver 5 pulses at 50 hertz on the commencement of a sweep. A four channel oscilloscope was also triggered from this device. The stimulator being driven by the Digitimer reproduced the 5 pulses. The pulse width was set to 1ms.The shortest time interval between stimulus trains was 4 seconds. As these experiments were investigating modulation of reflex pathways by altering head, neck and elbow joint position a test was only instigated once sufficient time for dynamic effects, resulting from the position change, had elapsed. Thus an interval of at least 30 seconds following a position change was employed before a test.

Flexion reflexes and crossed extensor reflexes were investigated following changes in head, neck and elbow joint position in cats with intact labyrinths and hemilabyrinthectomized cats.

2.3.0 Data recording, storage and analysis.

In the following sections details will be given of the forelimb muscles studied, the technique used to record the activity of these muscles and the subsequent analysis of recorded data. Details of methods used to record eye movements in acute and chronic hemilabyrinthectomized preparations will also be given.

2.3.1 Forelimb muscles.

Labyrinth and neck reflexes, as previously described are unlikely to influence only one group of muscles. The pattern of naturally evoked labyrinth and neck reflexes have been well described for the medial head of triceps brachii, but little is known about the behavior of other forelimb muscles particularly the flexors. In this study of the organisation of labyrinth and neck reflexes the behaviour and relationship between extensors and flexors of the same and of opposite limbs were examined.

In order to study the behaviour of extensors and flexors in the one limb EMG recordings were thought most appropriate. EMG recordings benefit over other myographic techniques in that minimal surgical inervention is required

and the limb can be left virtually intact. Two pairs of EMG electrodes were placed into muscles of each forelimb. Normally one pair of electrodes would be placed in an extensor, the other in a flexor. The extensor muscle studied was usually the medial head of triceps. This muscle was regarded as a standard as labyrinth and neck reflexes have already been described in this muscle. Occasionally records of EMG activity were taken from the other two heads of triceps. For flexors both biceps and brachialis were studied. Biceps takes its origin from the supraglenoid tubercle of the scapula and runs along the cranial surface of the humerus before inserting, by a rounded tendon on the radial tuberosity of the radius. In consequence biceps is functionally assosiated with flexion of the forearm and supination of the hand. Brachialis is a less complex muscle spanning only the elbow. A 'V' shaped muscle, brachialis originates from the lateral surface of the humerus inserting on the ulna just distal of the semilunar notch. It is a clear flexor of the forelimb. During the course of an experiment records could be attained from any one or two sets of the four electrode pairs. This allowed comparisons to be made of extensor and flexor behaviour from one or both forelimbs during alterations in head or neck positions. In this manner the complete pattern of reflexes acting on the muscles studied could be built up. This procedure was carried out on acute and chronic hemilabyrinthectomized preparations as well as cats with intact labyrinths.

2.3.2 EMG recording.

Electromyograms (EMG's) of the above forelimb muscles were recorded in the following way. Pairs of silver wires insulated except for the tips were inserted into the belly of the appropriate muscles through 21-gauge hypodermic needles which were subsequently withdrawn. Fig. 4 shows the construction and method of implantation of this type of electrode. The EMG signal is then amplified (x500) and low pass filtered (low frequency cut off 100Hz). The signal at this point could be either viewed directly on a 4 channel storage oscilloscope or rectified and integrated prior to display. The time constant of the integrator could be set to 20,50,100,200,500 or 1000msec by way of a six position switch. The oscilloscope was used to display the EMG signals from any of two of the muscles under study at any one time. Head and neck position signals being displayed on the remaining two channels. With the oscilloscope set to a slow sweep speed (typically 1sec/div or slower), and on storage mode, polaroid photographs of EMG responses to changes in head or neck position could be taken. An output facility of the oscilloscope was, in addition, employed to make a permanent record of all experimental data by recording the raw EMG and position signals on tape (Hewlett and Packard 3960 FM magnetic tape recorder). By recording the untreated EMG signal it was possible to subsequently analyse the EMG's in greater detail once the experiment had been completed. Graphic representation of recorded EMG was obtained by either

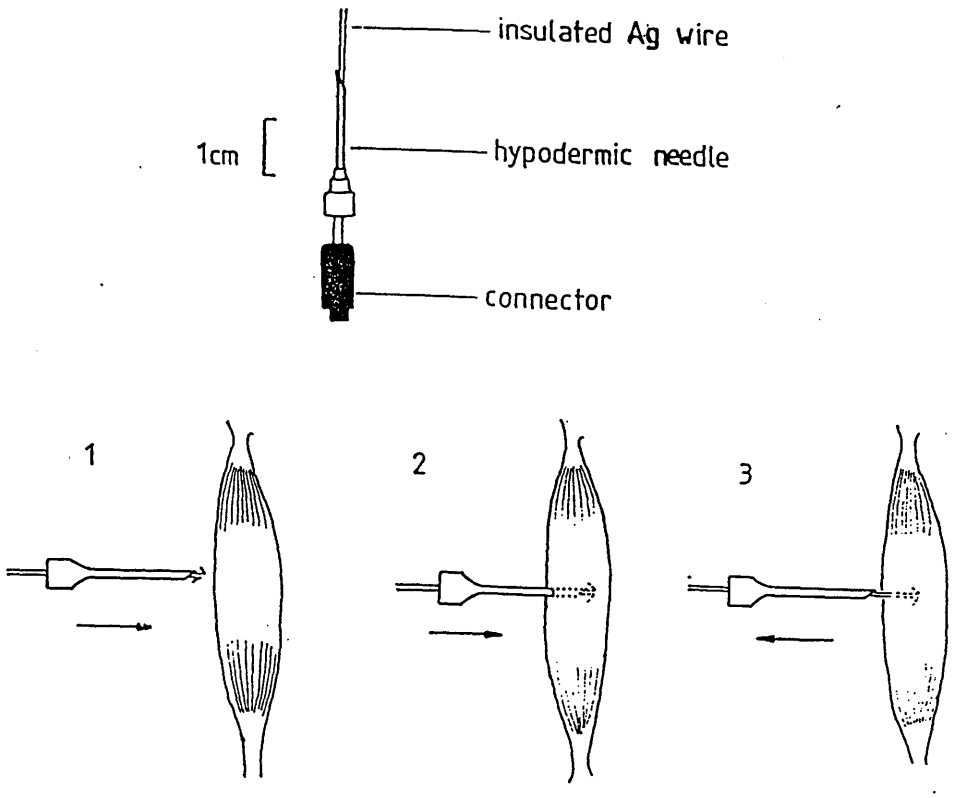


Figure 4. Diagram showing construction of EMG electrodes and method of insertion into muscular tissue.

photographing the replayed record or by playing the tape to a pen recorder. By replaying the untreated EMG various manipulations such as full wave rectification and integration of the signals can be carried out without losing any quality from the original signal.

2.3.3 Nystagmus in acute and chronic hemilabyrinthectomized cats.

A consequence of hemilabyrinthectomy is the generation of a nystagmus. This nystagmus is observed in the acute preparation but disappears after approximately 48 hours in the chronic preparation only to reappear following decerebration. These horizontal eye movements are monitored by recording the electrooculogram (EOG). EOG recordings are obtained through 3 silver, silver chloride electrodes placed at sites around the orbits. Fig. 5 illustrates the placement of the electrodes. These electrodes are simply pushed through the skin covering the lateral extents of the orbits and through the skin between the orbits, over the bridge of the nose. Due to the synchronized muscle activity which generates the eye movements the electrical activity picked up by the electrodes from these muscles is directly related to eye position. This activity is amplified and filtered. A DC coupled differential amplifier with a flat response from DC to 7.5KHz (-3dB cut off) and a gain of 100 is used. The signal is then high pass filtered and displayed on the oscilloscope and samples of the EOG recorded on magnetic tape. The nystagmus recorded in this

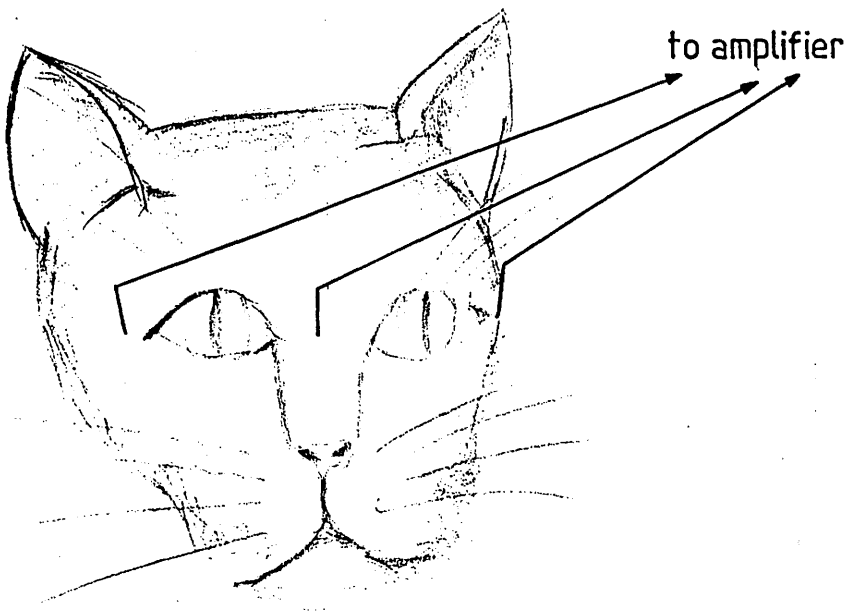


Figure 5. Drawing illustrating placement of electrodes for recording horizontal eye movements, (the central electrode is common).

way can be seen to be composed of two components, a fast and a slow component. The frequency, amplitude and direction of the eye beats can be obtained from such records.

CHAPTER 3 Results.

The results to be presented describing labyrinth and neck reflex organisation are divided into three sections: (1) labyrinthine and neck reflex organization in normal, (2) acute and (3) chronically hemilabyrinthectomized cats. The effect of altering limb position on these reflex systems in normal and acute cases will be dealt with separately.

3.1.0 The normal pattern.

Labyrinth and neck reflexes were studied in 26 decerebrate cats with intact labyrinths. The results to be presented, that detail the pattern of labyrinth and neck reflexes are based on this group of animals.

3.1.1 Labyrinth reflexes in cats with intact labyrinths.

Labyrinthine reflexes were studied in isolation from neck reflexes following denervation of cervical joints (methods section 2.1.3). The terminolgy used to describe the adequate stimulus is as defined in the Methods section.

Tilting the head of a decerebrate cat, under suitable conditions, results in clear signs of movement in all limbs (both fore and hindlimbs). These movements are generally more easily observable in the forelimbs. With the head tilted toward one side of the animal the limbs of that side become more rigid while the limbs on the opposite side

appear to show a reduction in rigidity.

Close observation of a decerebrate cat following a head tilt reveals, that although alterations in the extensor tone of the limbs is apparent these muscles are not the only muscles cooperating in the response. In active preparations strong flexor activity can be seen following head tilts. The strength of these observable changes in muscular activity can be seen to vary with the excitability of the preparation as judged by the amount of spontaneous EMG and the presence of brisk withdrawal reflexes. The changes are absent when the excitability is low or during periods when there is extreme extensor rigidity. Excitability changes in a decerebrate preparation can vary substantially during the course of any one experiment, ranging from periods of intense rigidity to periods where the limbs are flaccid and offer little resistance to passive displacment. In describing the reflex response of forelimb muscles to changes in head position an attempt will be made to correlate changes in reflex behaviour with alterations in the excitability and condition of the preparation. The behaviour of forelimb extensors shall be considered first.

3.1.2 Labyrinth reflexes in extensor muscles of the forelimb.

In a previous study Lindsay (1975) described changes in the length of the medial head of triceps following changes in head position. In this present study

the electrical activity of this muscle and of the other two heads of triceps were sampled under isometric conditions. Electromyographs (EMG) were recorded from right and left forelimbs. Records of EMG activity in the extensor muscles on lateral head tilts revealed the same pattern of extensor activity as seen by Lindsay (1975). With the axis vertebra clamped and the head rotated away from the normal position the EMG activity in extensors from opposite forelimbs displays, in the majority of the cats studied, reciprocal alterations in EMG behaviour. In the right forelimb a head rotation to the left leads to a suppression of EMG activity in the three heads of triceps on that side. While in the equivalent group of muscles on the left side a marked increase in EMG is seen during this head movement. Such behaviour is illustrated in Fig. 6. In this figure head position is indicated by the signal shown on the bottom trace, the EMG's from right and left triceps by those of the top and middle traces, respectively. The reciprocal behaviour of the extensors of the opposite forelimbs is clearly demonstrated in this figure. The figure also demonstrates the long lasting nature of the reflex response to a positional head change. By examining firstly the nature of the EMG behaviour of the right extensor it is apparent that following the head rotation from the normal position to a position 30 degrees to the left there is a gradual decline in activity. The activity falls until the discharge level is considerably less than that observed at the normal position. The time course for this reduction of activity in this example is around 500ms. This suppression

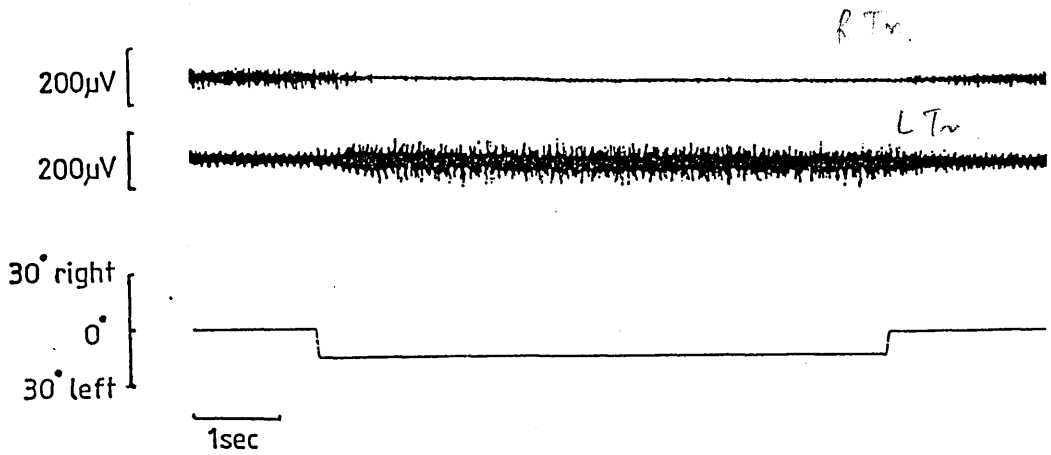


Figure 6. Labyrinth reflex in extensor muscles of opposite forelimbs. EMG recordings from triceps in the right (upper trace) and left (middle trace) forelimbs on rotation of the head to the left (lower trace):(decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

of the original level of activity is maintained for the remaining period the head is held in its new position (the positional change lasting just under 6.5 seconds). On returning the head to the normal position signs of increased EMG activity become apparent. As with the reduction in activity the reappearance of EMG is gradual and does not start to increase until after a considerable delay (approx 250ms). Simultaneously, the left triceps (Fig. 6, middle trace) shows behaviour reciprocal to that of the right triceps in its response to head tilt. Like the response in the right extensor the alterations in activity levels that follow from the head movements at the start, and end of the positional change develop slowly and are long lasting. The tonic increase in the activity of the left extensor (following the head tilt of 30 degrees to the left) is only apparent after approximately 250ms. During the positional change the increased activity in the left extensor can be seen to be tonic in nature, the EMG being maintained at an elevated level until the head is returned to the normal position. The contrasting behaviour of right and left extensor muscles (ie. decreased and increased EMG activities respectively on head rotation to the left) and the tonic nature of the activity changes occurring with the head tilt depicted in Fig. 6 are typical of labyrinth reflexes arising from the otolith organs as described by Lindsay (1975) and Lindsay et al. (1976). Although the responses just described are characteristic of otolith reflexes it is also common in addition to the slow onset of responses that the reflex response to a positional change

may be recognized to consist of a phasic component as well as a tonic one. Fig. 7a and 7b illustrate this other common feature of the reflex behaviour. As in Fig. 6 the reflex response of the right and left extensor (triceps) muscles (top and middle traces respectively) is consistent with the reflexes described by Lindsay (1975). The response in this example of the two extensors can be seen to contain phasic as well as tonic components.

By considering the right extensor response in Fig. 7a it can be seen that the gradual decline in activity apparent in Fig. 6 on head rotation to the left is replaced by an almost complete suppression of EMG activity following a latency of approximately 800ms. This reduction in EMG activity is maintained until the head is rotated toward the right; at which time following this movement the right extensor EMG shows a short lasting burst of activity before a new level of activity is established.The rapidity of the onset of this phasic burst of activity in Fig. 7a and the slow sweep speed employed make it difficult to measure with any great accuracy the latency of the response. It is clear however that in Fig. 7b which illustrates a similar response, though at a much increased sweep speed, that the phasic component is closely associated with the period of head movement. A similar situation is also apparent in the response of the left triceps in Fig. 7a. In this instance the initial response to the head movement is an early increase in activity (approx. 200ms). This increased activity is, however, not maintained but declines after approximately two seconds to a new resting level which

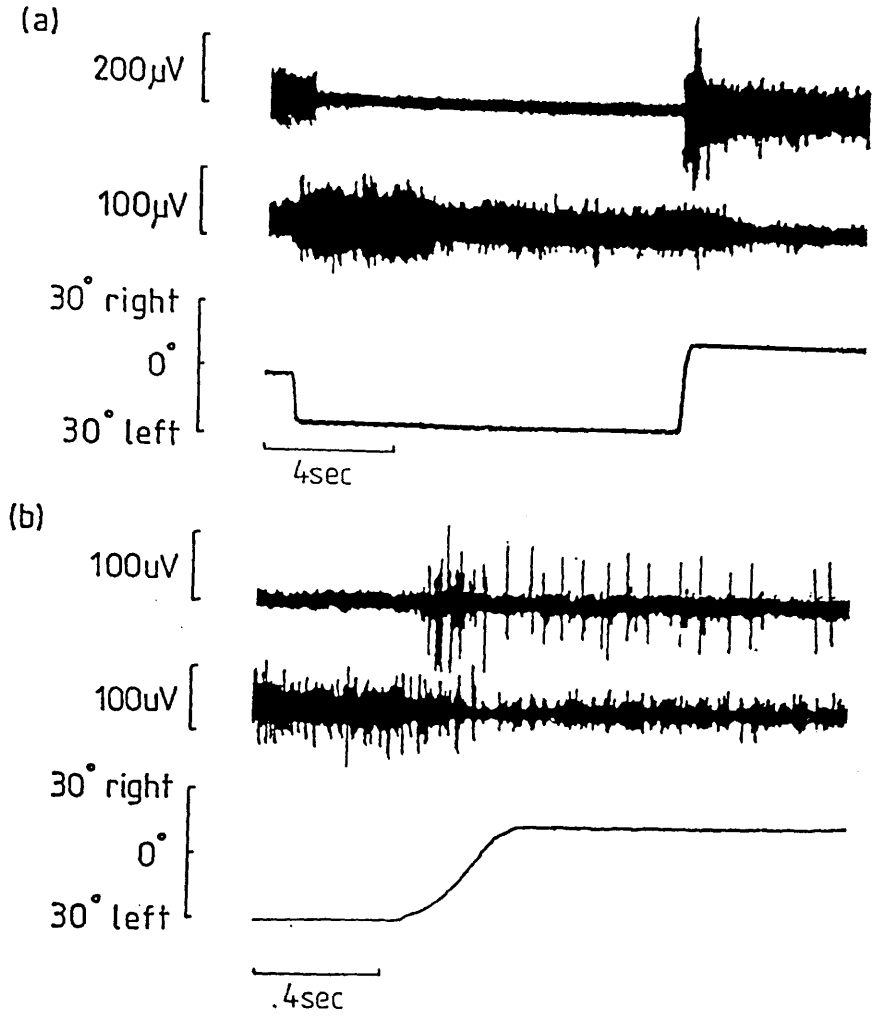


Figure 7. Labyrinth reflexes in right and left triceps. (a) and (b) EMG recordings from right and left triceps (upper and middle traces respectively in both (a) & (b)) on rotation of the head (lower trace). Note faster sweep speed in (b): (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

lasts for the duration of the positional change. This level of activity is however greater than that observed with the head in the mid-position. This type of behaviour, and of the more distinct phasic like response exhibited by the right extensor in Fig. 7 is commonly seen following changes in head position. The association with dynamic positional changes, coming at the start or finish of a head tilt, suggests that these phasic like responses result from the stimulation of semicircular canal afferents or from otolith units sensitive to velocity, although it is also possible that the responses reflect intrinsic properties of the motor units sampled from.

The tonic reflexes described by Lindsay (1975) show asymmetry in their organisation. Such asymmetry is evident from Fig. 7a. In this figure it should be noted that the head tilt does not return to the normal position but terminates with a movement to the 30 degrees right position. Thus this figure illustrates the EMG of right and left extensors at three head positions, these are: (1) normal, (2) 30 degrees left and (3) 30 degrees right. Different magnitudes of muscle activity are associated with each of these three positions. The right extensor showing least activity at the 30 degrees left position, intermediate activity at the normal position and greatest activity at the 30 degrees right position. The behaviour of the left extensor is reciprocal to this.

Figs. 6 and 7 illustrate the dropping in and out of motor units following head tilts. Increases in muscular activity can from these figures, and from ones to follow,

be suggested to result from both increases in the firing rate of already active units and from the recruitment of previously silent units. Similarly, reductions in activity, seen in extensors when the head is tilted away from the recording site, result from a drop in firing frequency of some units and the silencing of others. A good example of this type of behaviour is given in Fig. 8. In this figure decreases in the EMG's of the right and left extensors are shown following head tilts to the left and right, respectively. The behaviour of the right triceps (Fig. 8a) illustrates these features most clearly. With the head tilted to the left there is an obvious decrease in the rate of the large spike shown, this unit eventually silencing completely. Additionally, the smaller units, which remain active throughout the head tilt, show only a reduction in firing frequency. On returning the head toward the normal position, the smaller units again show an increased rate, while the larger unit is recruited a little later. It is perhaps interesting to note that of these units show distinctly different latencies are observed in response to the head tilt back to normal. The smaller units show a much more rapid response than the previously silent larger unit. The response of the larger unit lagging those of the smaller units by almost 1.5 seconds. This variability in latencies between these units illustrates a problem associated with trying to measure reflex latencies by EMG recordings. In these experiments the EMG samples a relatively small proportion of the muscle fibres that are influenced by the reflex actions from the labyrinth. In

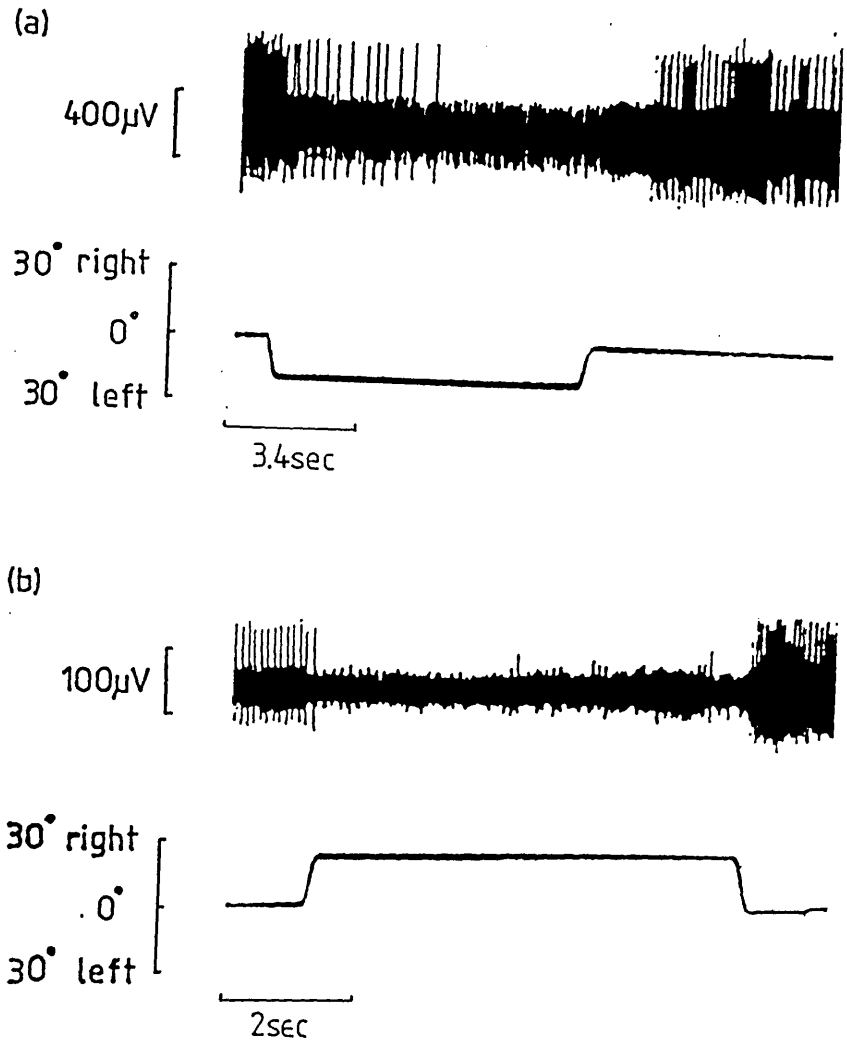


Figure 8. Labyrinth reflexes in the right triceps. (a) EMG recording from right triceps on head rotation to the left. (b) EMG recording from the left triceps on head rotation to the right. Note that EMG activity is reduced in both (a) & (b) despite opposite directions of tilt: (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

consequence it is impossible (with the tecniques employed) to know whether the response of a single unit is the earliest sign of reflex activity in that muscle. What is apparent from this type of recording, is that the reflex actions onto different motor units in one muscle, although acting in the same direction, are not equal in efficacy.

Fig. 8b also illustrates the behaviour of an extensor muscle to a head tilt that silences an active motor unit. In this instance, the EMG is from the left triceps and the head rotation is toward the right. Taken along with Fig. 8a the two responses from opposite limbs provide another example of the reciprocal interlimb relationship between extensors during lateral head tilts. The figure demonstrates reductions in activity in both the right (Fig. 8a) and left (Fig. 8b) triceps muscles. The reductions occur following head tilts that are in opposite directions. This figure demonstrates reductions in extensor EMG, accompanying side-up head tilts.

The behaviour of extensor muscles to changes in head position is dependant to some extent on the tonic or resting background activity seen in the recording. For bidirectional reflexes to be observed it is essential that significant activity is present at rest. Muscles showing no EMG activity can only show unidirectional reflexes (i.e., increased activity on side-down tilts), while muscles which are close to maximal activity can only show reductions in activity on side-up tilts, with side-down tilts having little effect, since the recorded motor units are near to maximal activity. These variations in behaviour will be

discussed in a following section. The extensor group of forelimb muscles, under appropriate conditions show asymmetric reflexes on tilting the head, these reflexes being organised reciprocally between limbs.

3.1.3 Flexor behaviour during natural labyrinth stimulation.

The previous section considered the behaviour of forelimb extensor muscles to natural labyrinthine stimulation, and has drawn on previous studies to illustrate agreement between results. In this section the reflex reactions of forelimb flexors to rotations of the head will be presented. The behaviour of flexors (biceps and brachialis) from both right and left forelimbs during positional changes of the head will be described and compared with reflexes observed in forelimb extensors.

Labyrinth reflexes were elicited by the same procedures as outlined earlier and were carried out free from neck reflex contamination following denervation of C1 and C2.

When recording from the left forelimb with EMG electrodes placed within either biceps or brachialis a correlation between muscular activity and head position can be recognized. Fig. 9(a and b) illustrates the response from the left biceps brachii (9a) and left brachialis (9b) to alterations in head position. With the head held in the normal position there is little spontaneous EMG activity from the left biceps. However, when the head is tilted away

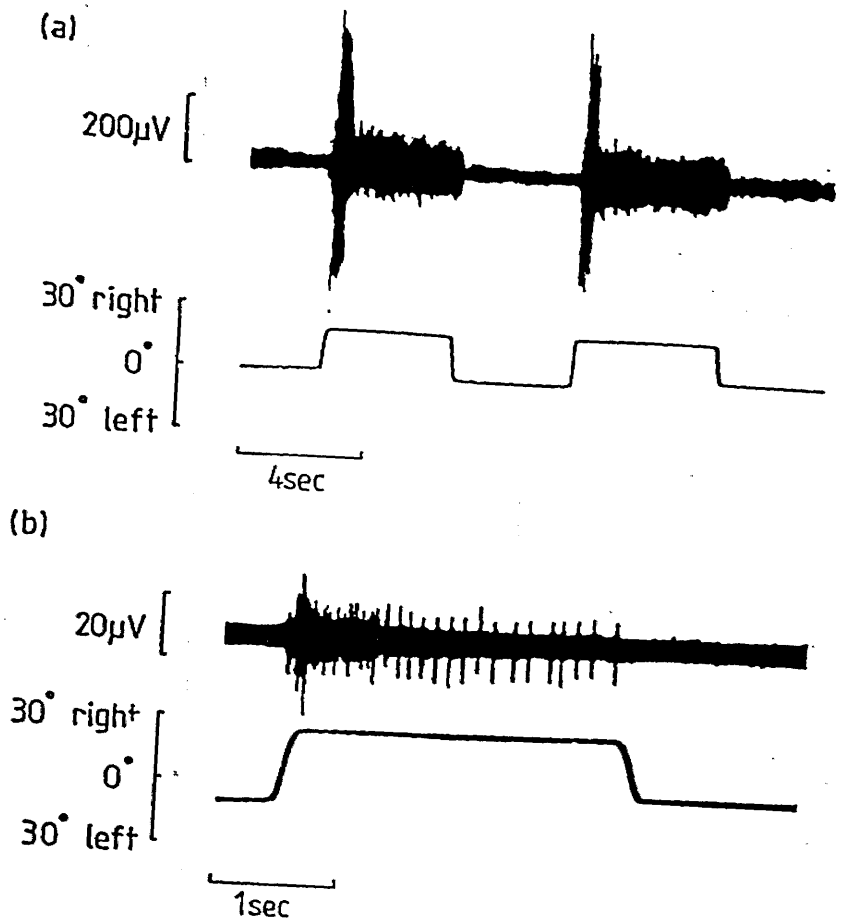


Figure 9. Labyrinth reflexes in a flexor of the left forelimb. (a) EMG recording from the left biceps brachii on rotation of the head, (b) EMG recording from the left brachialis on rotation of the head (lower trace in each example): (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

from the normal position toward the right there is a clear change in activity levels. In Fig. 9a two consecutive head rotations to the right are depicted. The response of the muscle is almost identical in both instances. Following the head tilt (20 degrees to the right) there is a large phasic burst of EMG activity followed by a period of sustained activity lasting, apparently without diminishing, until the head is returned to the normal position. On returning to the normal position, the EMG is again silenced. The EMG remains silenced until the head tilt is repeated. Like the responses shown by extensor muscles this figure demonstrates that head tilts can produce sustained flexor reflexes that correlate well with head position. The flexor response (Fig. 9a) shows a phasic burst, which is associated with the period of head movement, and an increased level of maintained EMG which is dependant on the static head position. Similar behaviour from the left brachialis is shown from a different preparation in Fig. 9b. In this instance the response is not as strong as those illustrated in Fig. 9a but serves to depict the phasic and subsequent tonic discharge recorded from the left brachialis on a head tilt to the right. The activity of an individual unit can be seen to persist for the duration of the head tilt.

With head movements toward the right of the animal the left flexor shows an increase in motor unit activity, moving the head in the opposite direction results in a reduction in the output of the muscle.

The response of the right flexor muscles are

organised reciprocally to the behaviour of the left flexors. Fig. 10 provides a demonstration of this reciprocal relationship between the labyrinth reflexes in flexors from opposite forelimbs. In Fig. 10a, a head tilt from 30 degrees right to 30 degrees left (bottom trace) is shown along with the response of left and right biceps brachiii (top and middle traces respectively). Prior to the head tilt the EMG from the left biceps shows distinct signs of activity while that of the right biceps is silent. Immediately following the change in position alterations in EMG activity in both muscles can be seen. In the left biceps the activity level is substantially reduced while the previously silent EMG of the right flexor shows considerable activity. A head tilt of the opposite sense is shown in Fig. 10b. In this figure the responses of the left and right biceps are again represented by top and middle traces, respectively. The head tilt illustrated in Fig. 10b is from a position of approximately 20 degrees right to 20 degrees left, and results in reciprocal activity changes between flexors of opposite sides. In this example the silent left flexor becomes active and the previously active right flexor is silenced following the head tilt. Taken together these figures show two important aspects of the response of flexors to changes in head position. Firstly, the responses to any one tilt about the longitudinal axis are reciprocal between left and right limbs, and, secondly, the activity changes seen in the flexor muscles of the opposite limbs are directionally specific. That is, increased EMG activity will only occur in the right limb

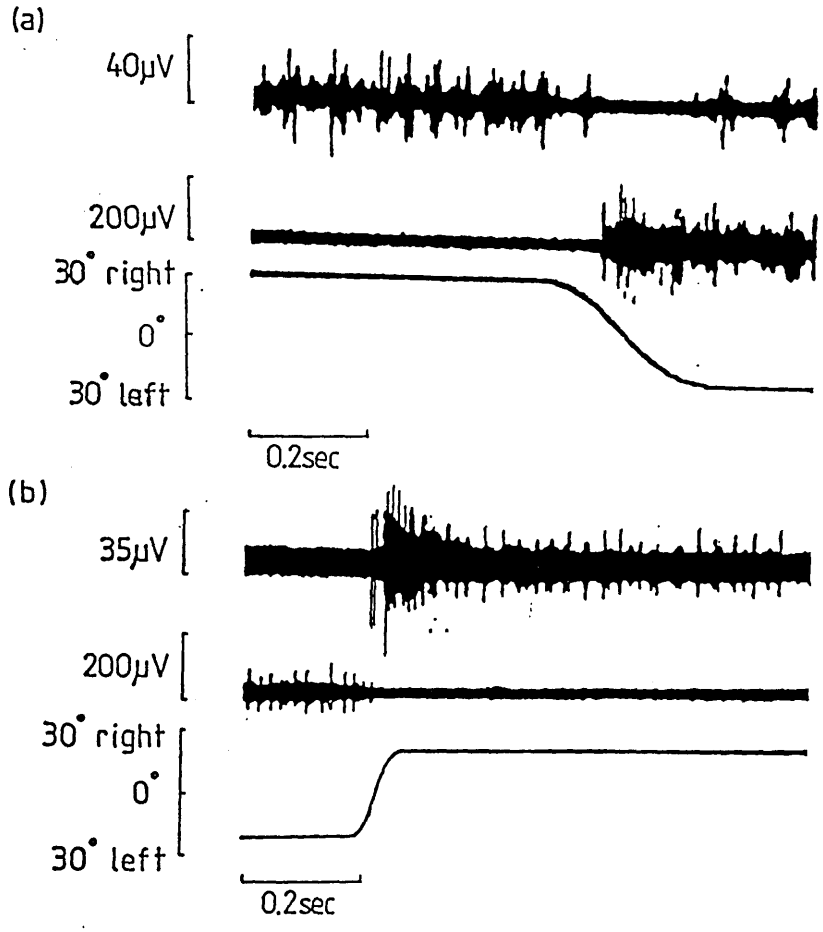


Figure 10. Labyrinth reflex in flexors from opposite forelimbs. (a) & (b) EMG recording from left biceps and right biceps (upper and middle traces respectively in (a) & (b)) on rotation of the head (lower traces). Note different directions of tilt in (a) & (b): (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

flexor when the head is tilted to the left (see Fig. 10a middle trace), whereas tilts toward the right result in a suppression of EMG activity (see Fig. 10b middle trace). While the inverse of this behaviour pattern is observed in the reflexes of the left flexor, that is, increased flexor activity occurs with rotations away from the limb (ie. toward the right, see Fig. 10b top trace) and decreased activity when the head is rotated toward the recorded limb (in this case a rotation of the head to the left, see Fig. 10a top trace).

A further example of the directional dependance in the labyrinth reflex is shown by the rectified and integrated EMG's illustrated in Fig. 11a, for the left biceps and Fig. 11b, for the right biceps. In both examples of reflex behaviour tonic activity changes can be observed following head tilts. In Fig. 11a and Fig. 11b head movements are in the opposite direction. That the respones to head tilt in the two flexor muscles illustrated are tonic in nature can be seen by the maintained increase in EMG activity that accompanies the head tilt. Once stabilized these sustained responses persist for the duration of the positional change (approximately 30 seconds).

In these examples of integrated flexor EMG the responses conform to the same pattern of reflexes as illustrated in the examples of the raw data. The advantage of displaying the integrated activity is that it is much easier to see how the motor units sampled are behaving over a long period of time. In Fig. 11b for example, during the

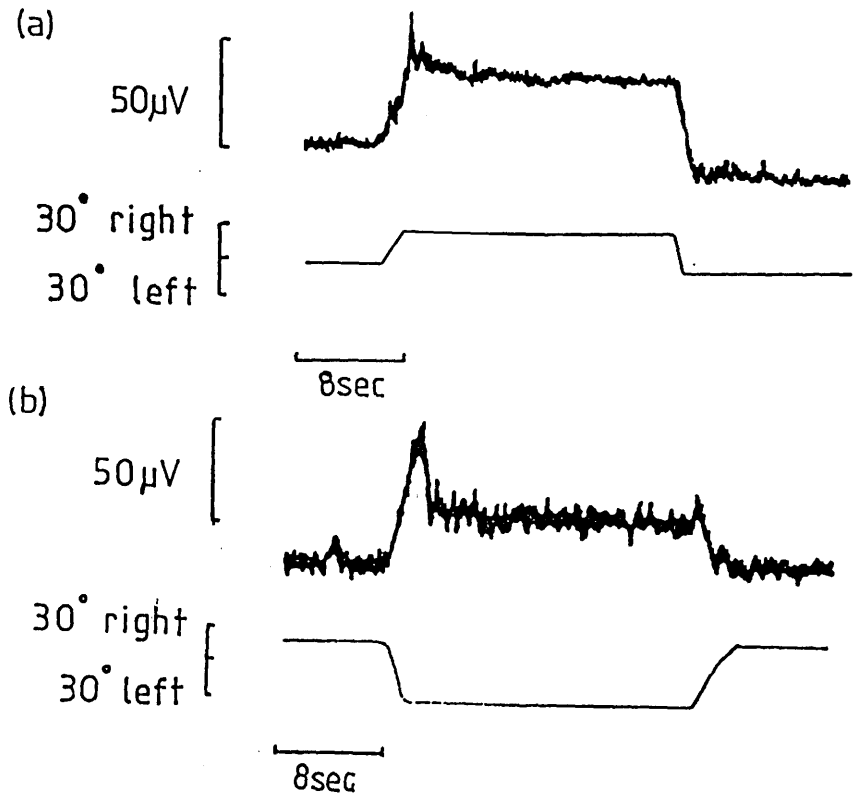


Figure 11. Labyrinth and neck reflex in left and right biceps. Rectified and integratated EMG from the left biceps (a) and right biceps (b) on rotation of the head to the right in (a) and to the left in (b), head position is shown by the lower traces: (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

initial movement to the left, the integrated EMG shows a steady increase in activity which peaks shortly after the movement ends. During the static portion of the tilt the EMG decreases slightly from this peak to a level (still greater than that at rest) which does not alter until the end of the static period. Whereupon the amount of EMG activity falls toward pre-tilt levels. By considering the shape of the response to the positional change the peak seen initially and the subsequent fall in activity from this maximum would seem to suggest that, in this example at least, the system shows greater dynamic than static sensitivity. This behaviour (see also Fig. 11a) may be the result of the dynamics of the labyrinthine receptors or may reflect properties of the motor units themselves or even those of the motoneurones and their synaptic input.

However the tonic responses shown are associated with the position of the head and, as stated above, provide clear evidence of sustained reflexes in forelimb flexor muscles folowing head rotations.

Labyrinth reflexes in the above figures have mainly been recorded from biceps brachii. These reflexes are similar in behaviour to reflexes recorded under similar circumstances in brachialis (a synergist to biceps). The next group of Figs. (12,13,14) serve along with Fig. 9b to illustrate that brachialis responds in a similar way to head tilts as biceps.

In Figs. 12,13 and 14 the response of the left brachialis is shown for head rotations to the right. The three figures are all from the same preparation and serve

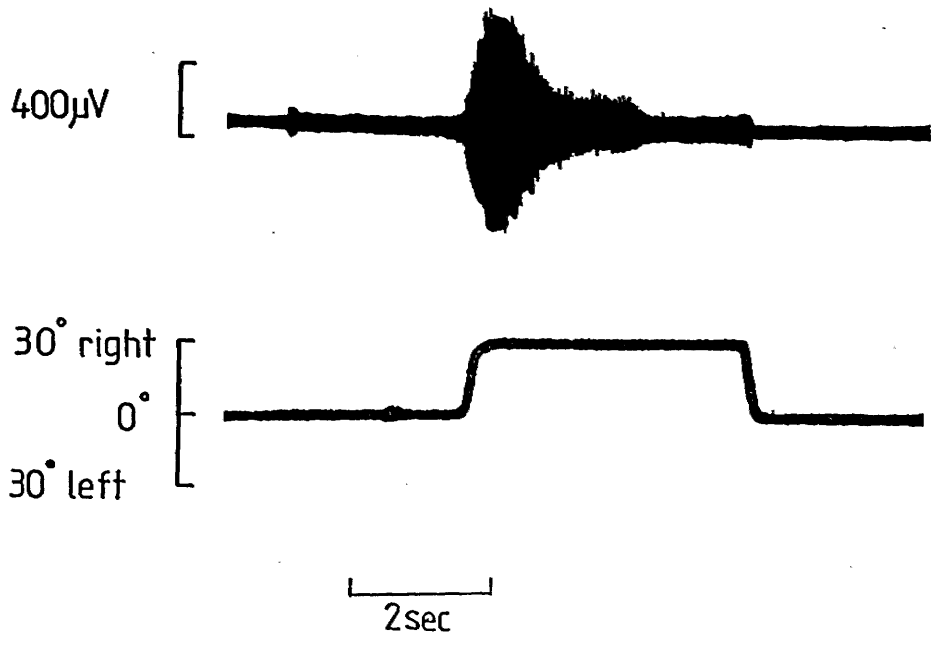


Figure 12. Labyrinth reflex in a flexor of the left forelimb. EMG recorded from the left brachialis on rotation of the head: (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

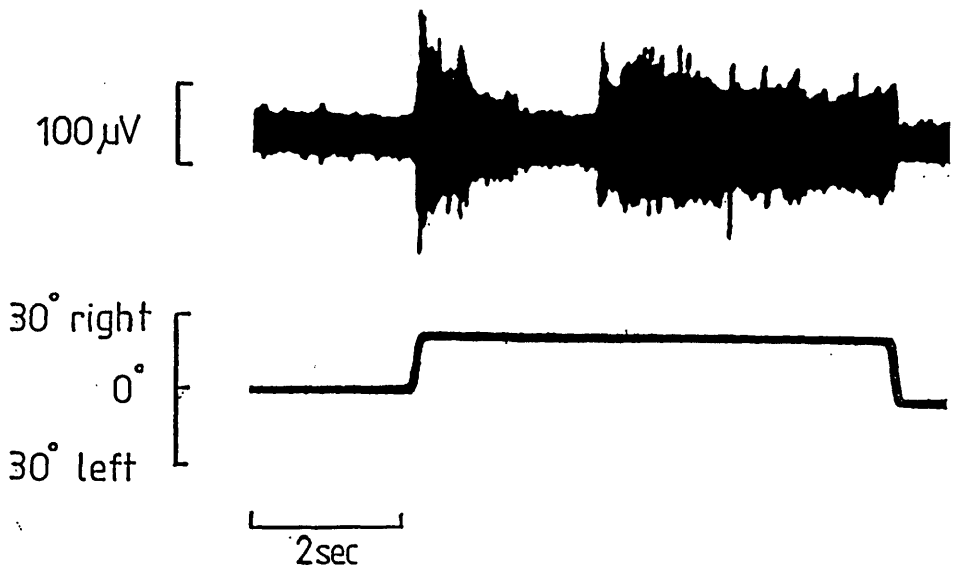


Figure 13. Labyrinth reflex in a flexor of the left forelimb. EMG recorded from the left brachialis on rotation of the head: (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

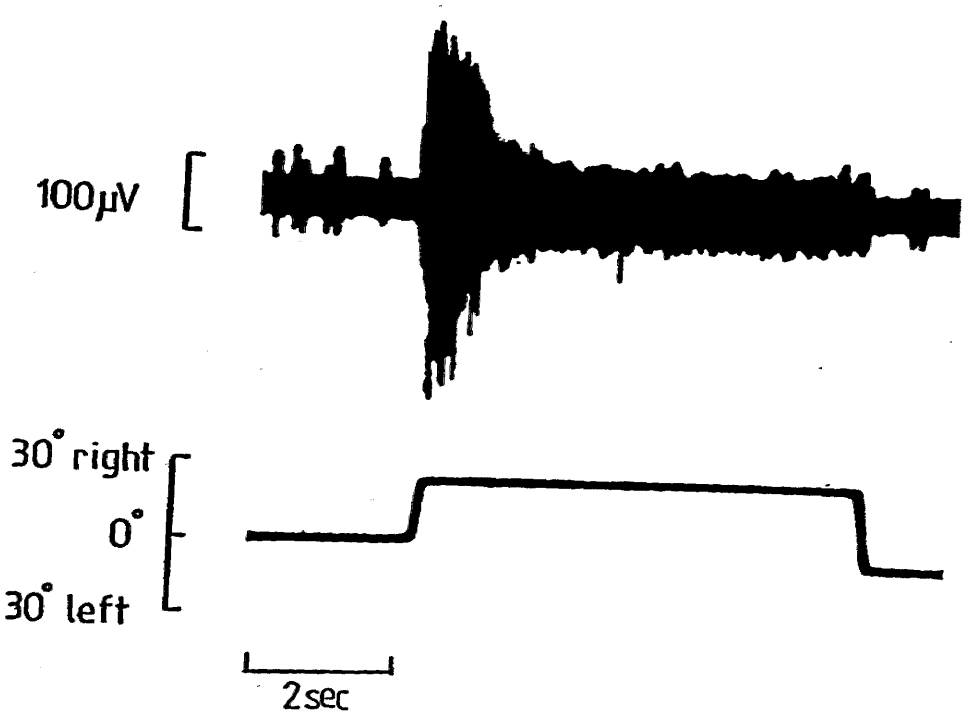


Figure 14. Labyrinth reflex in a flexor of the left forelimb. EMG recorded from the left brachialis on rotation of the head: (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

to illustrate not only similarities in response to biceps, but also to demonstrate that these reflexes can show considerable variation in form during the course of an experiment. Despite the variability in the form of these reflexes, in all three examples the head tilt to the right produces signs of increased flexor activity. Although variable in shape and size the direction of the reflex responses to head tilt is consistent. In each of the figures a prominant phasic response in the EMG can be identified following the head tilt, and although this varies in size, it does not show the same variability as is evident for the tonic component. Indeed in Fig. 12 there is no significant tonic discharge of motor units following the head tilt. Tonic activity is however evident in the responses shown in Figs. 13 and 14. In Fig. 13 the phasic component of the response has subsided prior to the onset of a tonic response, this occurs almost three seconds after the initial positional change. The EMG on returning to the normal position is immediately silenced. While in Fig. 14 no equivalent delay in the tonic response of the muscle is observed. The tonic response to the positional change fusing with the phasic EMG component. The EMG silencing on returning the head to the normal position. Such variability in the behaviour of an individual muscle during the course of an experiment is commonly encountered, and in many cases a response may be absent altogether following a head rotation. However when present the pattern of activity in biceps and brachialis is similar and is characterised by an increase in the motor output during head rotations away

from the recording side and decreases with rotations toward the recording.

3.1.4 The relationship between labyrinth reflexes recorded in forelimb extensors and those from the flexor muscles.

How then does the activity of the flexors described above (section 3.1.3) compare to the reflex behaviour of extensor muscles during natural labyrinthine stimulation.

Facilitation of a forelimb extensor occurs when the head is rotated toward the recorded muscle (ie. a side-down tilt) while a suppression of muscular activity occurs with rotations directed away from the recording site (ie side-up tilts). The behaviour of forelimb flexor muscles to positional changes of the head reflect the opposite behaviour. This reciprocal relationship between antagonist muscles of the forelimb is illustrated in Fig. 15.

In Fig. 15 a and b the reflex responses of both triceps and biceps are shown for left (Fig. 15a) and right (Fig. 15b) forelimbs following an approximately 30 degrees head rotation toward the right. Fig. 15a shows that the EMG activity in the left triceps(Fig. 15a upper trace) decreases while that in the left biceps (Fig. 15a middle trace) increases following a head rotation to the right. The responses from the same muscles in the right limb, for the same direction of head rotation are shown in Fig. 15b, and are seen to be in the opposite direction to those occuring in the left limb. For example, the EMG in the left biceps increases (Fig. 15a, middle trace), while that in

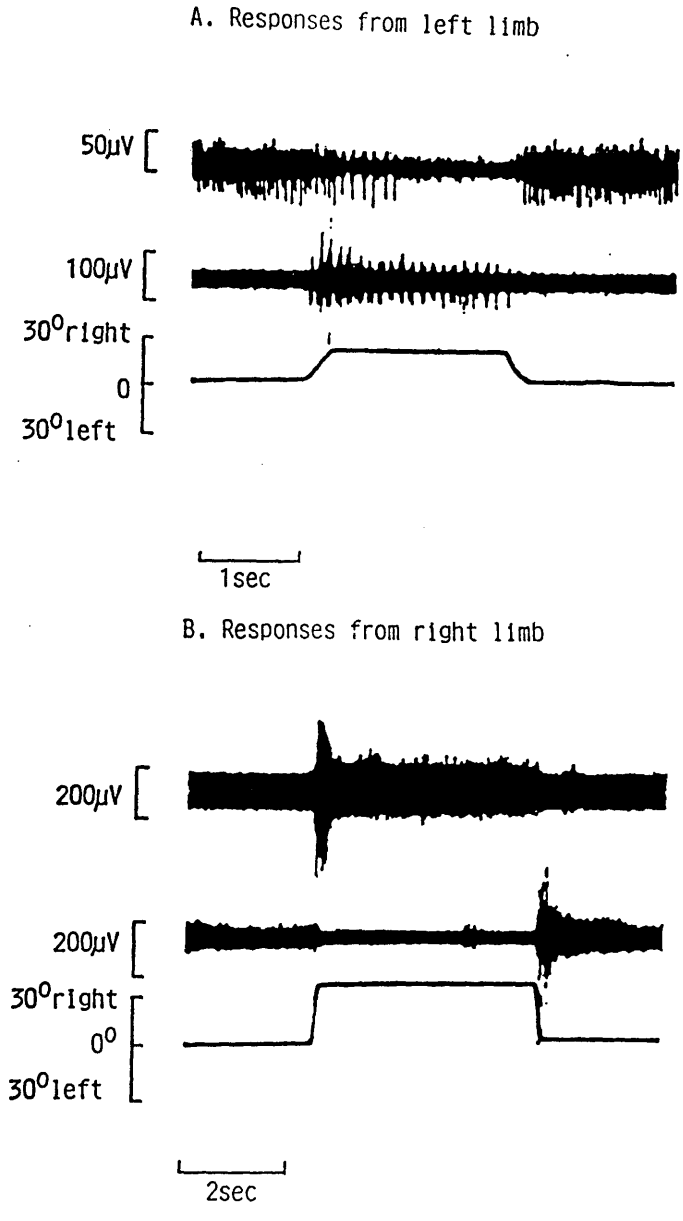


Figure 15. Pattern of labyrinth reflexes in extensor and flexor of both forelimbs. EMG from triceps (upper trace) and biceps (middle trace) from left forelimb (A) and right forelimb (B) on head rotation to the right (lower traces in (A) & (B)): (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

the right biceps (Fig. 15b, middle trace) decreases following a rotation of the head toward the right. Therefore, within the same limb the labyrinth reflex is organized reciprocally between triceps and biceps (Fig. 15 a and b), whereas in the right and left forelimbs the labyrinth reflex from triceps in one limb and biceps in the other operate in the same direction (e.g. cf. Fig. 15a middle trace with Fig. 15b, upper trace). An example of the synchronous activation between triceps in one forelimb and biceps in the other forelimb is given in Fig. 16. In this example a head rotation to the right generates excitatory labyrinth reflexes in the right triceps (Fig. 16, upper trace) and in the left biceps (Fig. 16, middle trace). The result is a synchronous extension of the right limb and flexion of the left limb. Thus with lateral tilts flexors and extensors from opposite limbs show either a synchronous activation or depression, depending on the direction of the head tilt. As a rule, therefore, labyrinth reflexes produce extension in a limb when the head is tilted toward that limb and flexion when the head is rotated away from that limb.

labyrinth reflex: side-down tilt = extension
side-up tilt = flexion

The pattern of reflex behaviour resulting from head tilts to the right and to the left for both forelimbs is summarised in table I. In this table an upward pointing arrow indicates increased EMG activity, a downward pointing

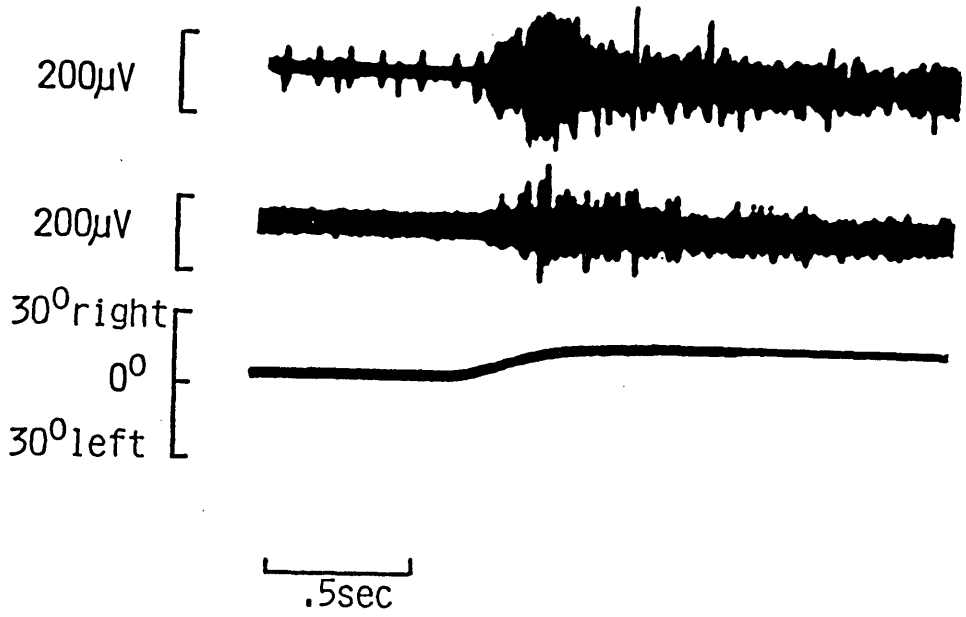


Figure 16. Labyrinth reflex 'coactivation' of extensor and flexor from opposite limbs. EMG from right triceps (upper trace) and left biceps (middle trace) on head rotation to the right (lower trace): (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

	Normal			
	Right limb		Left limb	
	Extensor	Flexor	Extensor	Flexor
Head rotation to right	↑	↓	↓	↑
Head rotation to left	↓	↑	↑	↓

Table I. Summary of effects produced by rotations of the head on the EMG activity of elbow extensors and flexors in cats with intact labyrinths. The arrows indicate increased or decreased activity.

arrow indicates suppression of EMG activity. These arrows representing contraction and relaxation, respectively.

3.1.5 The pattern of reflex behaviour of extensors and flexors following natural stimulation of the neck proprioceptors.

In this section reflexes acting on forelimb muscles following rotation of the neck will be described and contrasted with the reflex actions of the labyrinth on these muscles. Neck reflexes were evoked in cats with intact labyrinths by fixing the head in the normal position and either rotating the axis vertebra to the right or left. In these preparations C1 and C2 dorsal roots were sectioned during the surgical preparation of the animal. The reflex response of muscles to this stimulus therefore arises from the activation of receptors below the C2 level. In addition, neck reflexes were also examined in a bilaterally labyrinthectomized cat. To produce neck reflexes in this preparation the innervation of the neck was left intact and the atlas vertebra clamped. By fixing this clamp and rotating the head, torsion of the atlanto-occipital and atlanto-axial joints occurs and this acts as the stimulus to the neck reflex pathways. The stimulus in the labyrinthless cat differs from the denervated neck preparation in that the stimulus acts through C1 and C2, whereas in the denervated preparations rotation of the atlas acts on receptors located below C2.

Recent experimental studies on neck reflexes

(Lindsay, 1975; Lindsay et al., 1976; Ezure & Wilson, 1983) have confirmed Magnus's (1926) observations on the action of neck reflexes to extensors. In this study the neck reflex action on extensors and flexors of the forelimb were examined.

The behaviour of flexors and extensors in the two types of preparation used showed qualitatively similar neck reflexes. Rotation of the axis vertebra with the head fixed produced clear alterations in the EMG in both triceps and biceps. The direction and form of the change in EMG activity was in agreement with previous descriptions of neck reflexes acting on extensor muscles (Lindsay et al., 1976; Ezure & Wilson, 1983).

3.1.6 Neck reflexes in forelimb extensors.

In the right limb rotation of the axis vertebra in cats with intact labyrinths (C1 and C2 cut) results in increased extensor EMG activity when the rotation is directed towards the left. In Fig. 17 such behaviour is illustrated for the right triceps following rotation of the axis vertebra to the left (Fig. 17a) and to the right (Fig. 17b). The integrated EMG is also represented in this figure by the middle traces. In Fig. 18 a neck reflex suppression of EMG activity from the left triceps is depicted following a rotation of the neck to the left. In this figure the EMG becomes silenced during the time the neck is held in the 30 degrees left position, the EMG reappearing on returning the neck to the normal position. By comparing Fig. 17a and Fig.

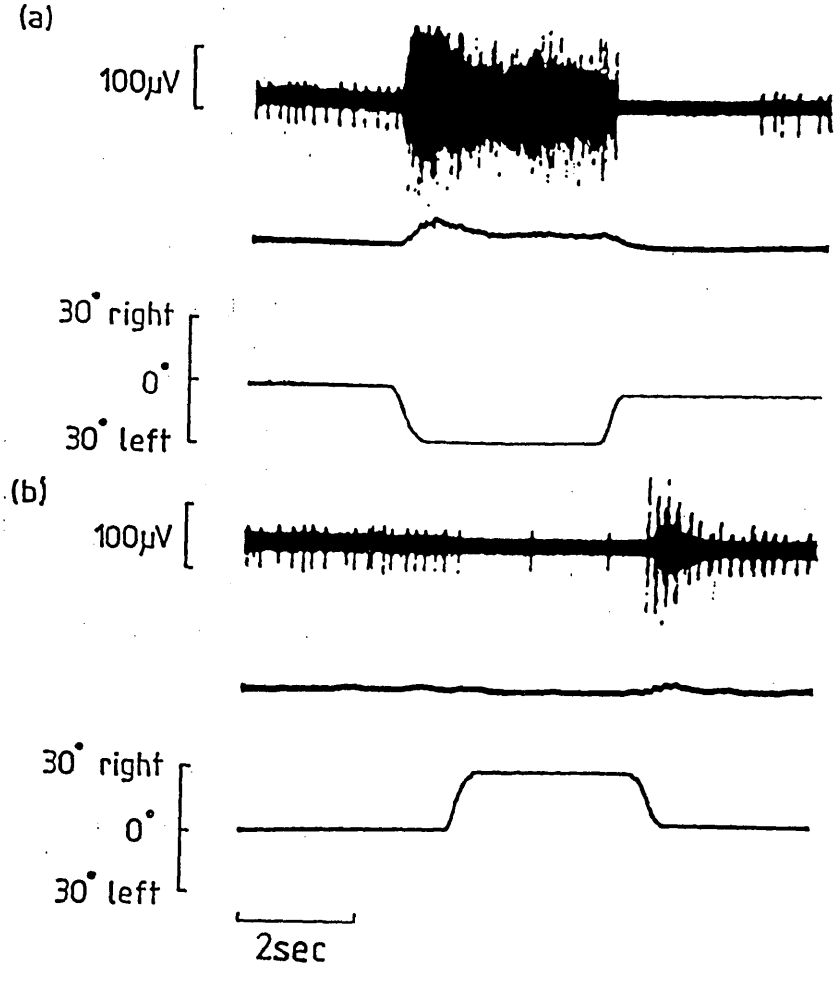


Figure 17. Neck reflex in the triceps of the right forelimb. EMG from right triceps, with rectified and integrated response below on rotation of the neck (axis vertebra) to the left in (a) and to the right in (b), neck position is illustrated by the lower traces: (decerebrate cat, intact labyrinths, C1 & C2 cut, head fixed in normal position).

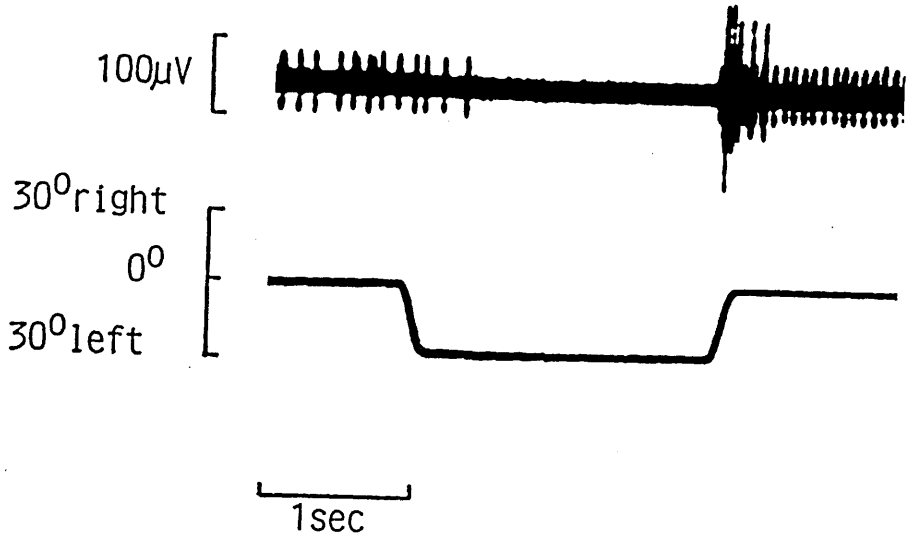


Figure 18. Neck reflex in an extensor of the left forelimb. EMG from left triceps (top trace) on rotation of the neck (axis vertebra) to the left (bottom trace): (decerebrate cat, intact labyrinths, C1 & C2 cut, head fixed in normal position).

18 the asymmetry in the organisation of neck reflexes between extensors from opposite limbs can be seen. In these two examples the neck rotation is to the left but the EMG responses in each case are opposite. A tonic increase in activity occurring in the right triceps (Fig. 17a) while a tonic decrease in EMG from left triceps (Fig. 18) is observed. The figures taken together provide an illustration of the asymmetry in the behaviour of extensors in one limb to neck rotations of opposite direction (Fig. 17), and of the reciprocal interlimb organisation of extensors from opposite limbs (Fig. 17a and 18).

Like the labyrinth reflexes discussed earlier the neck reflex also exhibits phasic components in the EMG response. The phasic bursts of activity are commonly associated with the appearance of large spikes following a positional change and are not evident throughout the time of EMG sampling. It is possible that these spikes represent motor units that are only recruited during the movement, that is during the period of time when the stimulus contains positional and velocity features. This however cannot be fully tested as yet due to the poor understanding of the site of the receptors involved in generating neck reflex afference.

3.1.7 Neck reflexes in forelimb flexors.

Rotation of the axis vertebra with the head fixed produces alterations in the EMG of forelimb flexors as well as extensors. An example of the reflex alteration of the

EMG activity in a flexor of the forearm is shown in Fig. 19. Here the EMG of the flexor brachialis is shown during a 20 degrees rotation of the neck toward the right. This movement results in a sustained increase in EMG activity, which on returning the neck to the normal position begins to diminish. A small phasic component can be recognised at the onset of the response. This phasic onset in the response is more evident in the example shown in Fig. 20 which illustrates the response in the left biceps to a neck rotation to the left. In this example the early part of the position signal is obscured by the magnitude of the EMG response. Despite this it is clear from this figure that this strong response to neck rotation is composed of two components, one phasic and one tonic. The tonic response enduring for the time of the positional change. Two further examples of the EMG response of the right biceps are shown in Fig. 21. Again, this figure illustrates increased EMG activity with neck rotations to the right. Though in Fig. 21b the response is predominantly phasic in nature with only minimal tonic activity apparent.

These examples of flexor reflex activity illustrate the degree of variability within the behaviour of these muscles to changes in neck position . The responses ranging from only a phasic component being present to responses comprising both phasic and tonic features. In some instances during the course of an experiment neck rotations would fail to evoke any observable signs of reflex activity (this also being true for head tilts occasionally failing to evoke labyrinth reflexes). In these instances it was

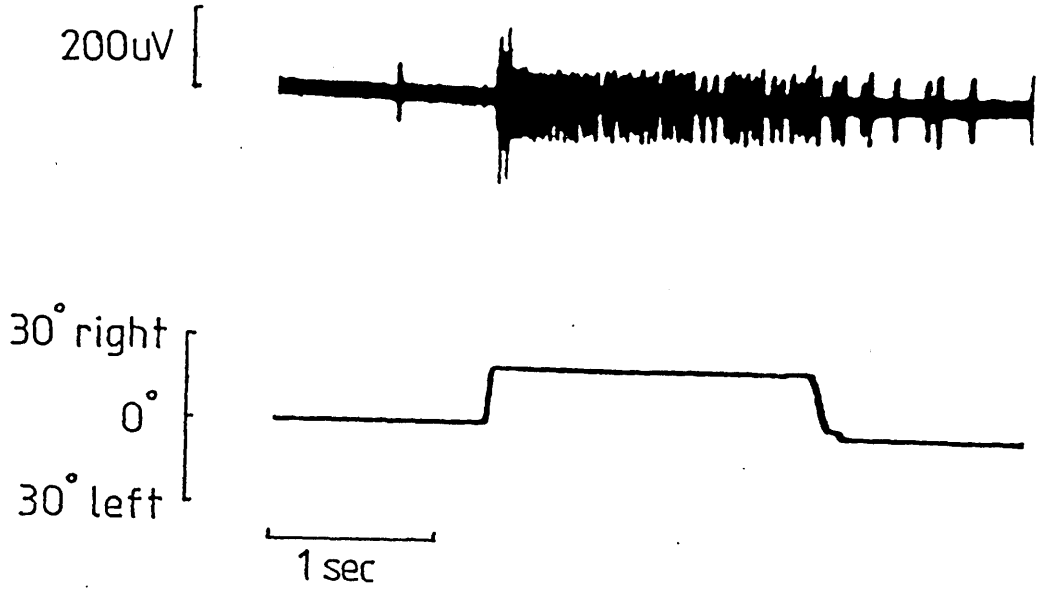


Figure 19. Neck reflex in a flexor of the right forelimb. EMG from right brachialis (upper trace) on rotation of the neck (axis vetebra) to the right (lower trace): (decerebrate cat, intact labyrinths, C1 & C2 cut, head fixed in normal position).

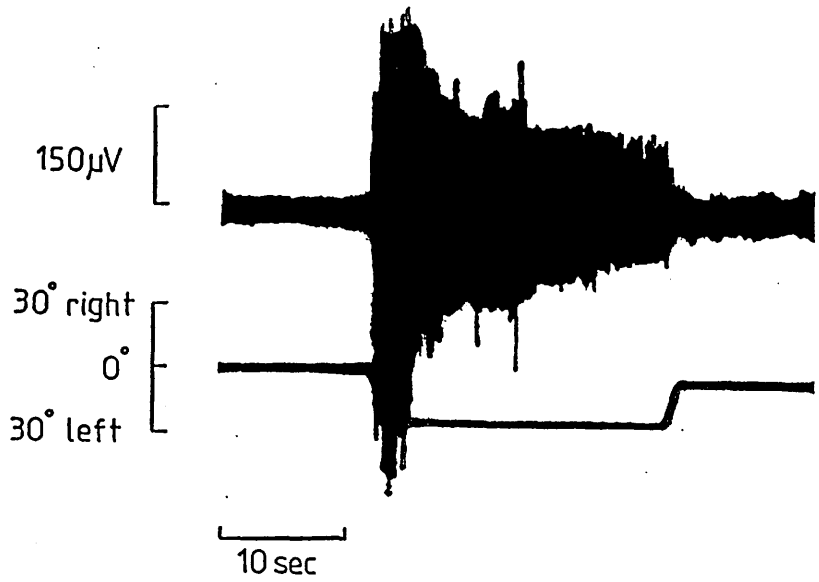


Figure 20. Neck reflex in a flexor of the left forelimb. EMG from left biceps (upper trace) on rotation of the neck (axis vertebra) to the left (lower trace): (decerebrate cat, intact labyrinths, C1 & C2 cut, head fixed in normal position).

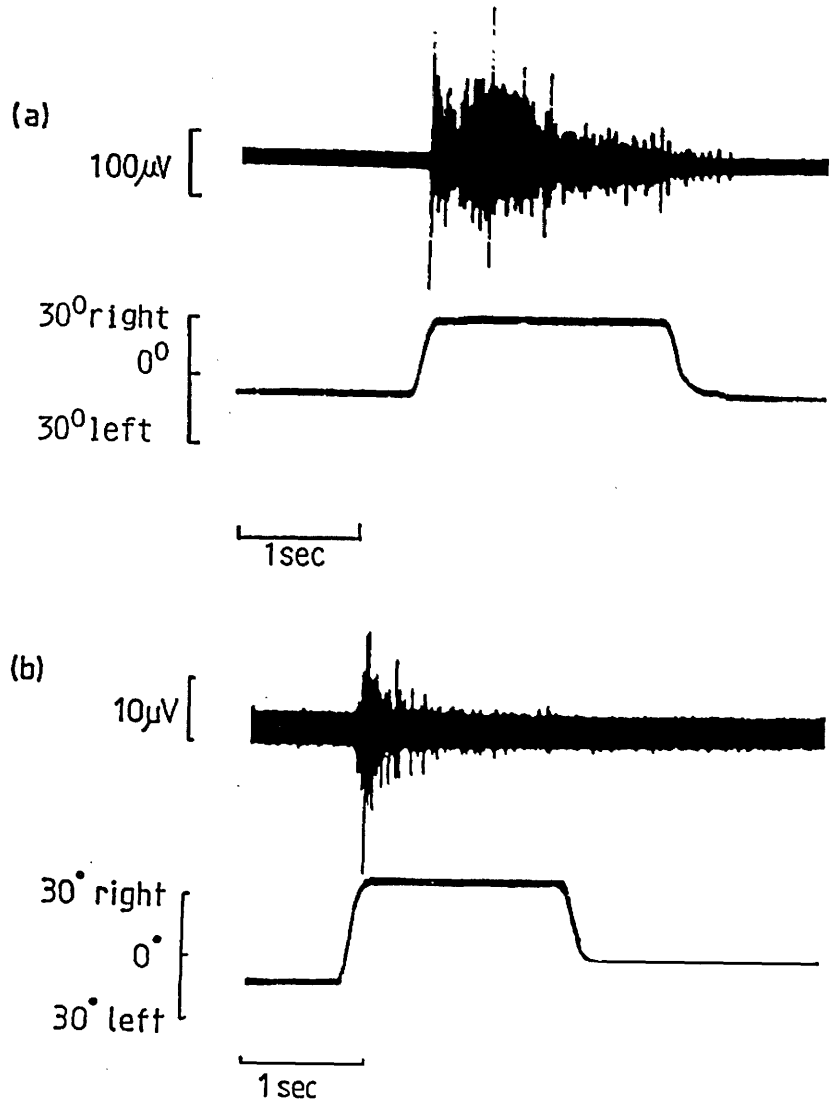


Figure 21. Neck reflexes in right biceps. (a) and (b) EMG activity from right biceps (upper trace) on neck rotation (axis vertebra) to the right (lower trace): (decerebrate cat, intact labyrinths, C1 & C2 cut, head fixed in normal position).

usually possible to relate these failures to the level of decerebrate rigidity present in the animal at that time (see later).

The figures detailing the flexor response to neck rotations have only shown the response to rotations that increase the discharge of motor units. In many experiments only unidirectional reflexes could be observed on rotations of the neck due to the lack of background discharge at the normal position. The consequence of this is that rotations in one direction exclusively activated previously silent motor units (rotation toward the recording site) while rotations in the opposite direction had no effect on the EMG trace. In preparations showing a degree of resting flexor activity neck rotations were observed to show bidirectional responses. With rotations toward the flexor muscle under study an increase in EMG activity was observed (as has been shown previously), while with opposite rotations a decrease in activity is observed. An example of such a decrease is shown in Fig. 22 where the integrated EMG from the right brachialis is shown during a rotation of the neck toward the left. The figure shows a reduction in flexor activity following the rotation and a subsequent recovery of activity toward resting levels on returning the neck to the normal positon. Together with the previous figures illustrating neck reflex behaviour in the right flexor it is clear that rotations to the right facilitate flexor EMG while rotations to the left suppress EMG activity.

As with the organisation of neck reflexes to

Figure 22. Neck reflex in the right biceps. Rectified and integrated EMG from right biceps (upper trace) on neck rotation (axis vertebra) (lower trace): (decerebrate cat, intact labyrinths, C1 & C2 cut, head fixed in normal position).

extensors, the right and left flexor muscles show reflex reactions that are opposed. Thus the flexors biceps and brachialis on rotation of the neck to the right show a reduced EMG in the left forelimb while in the right limb these muscles show increased activity. Therefore by recording from flexors in opposite limbs during neck rotation a reciprocal relationship can be seen to operate. Fig. 23 illustrates this reciprocity. A continuous side to side movement of the neck is shown to modulate the EMG of left (top trace) and right (middle trace) biceps. When the neck moves toward the left, the left biceps' EMG shows increased activity while that from the right biceps is decreased. This pattern of activity reverses when the neck is moved in the opposite direction.

Figs. 19-23 illustrate that neck reflexes are present in flexor muscles of the forelimbs and that they are organized reciprocally between flexors from opposite limbs.

3.1.8 The relationship between neck reflexes recorded from flexors and those recorded from extensors. A comparison between cats with and without labyrinths.

The pattern of reflex behaviour described for flexors during neck rotation is opposite to that described for forelimb extensors under similar conditions. Thus it would seem that within the same limb the neck reflex is reciprocal between flexor and extensor. This can be seen from the EMG traces illustrated in Fig. 24, obtained from a

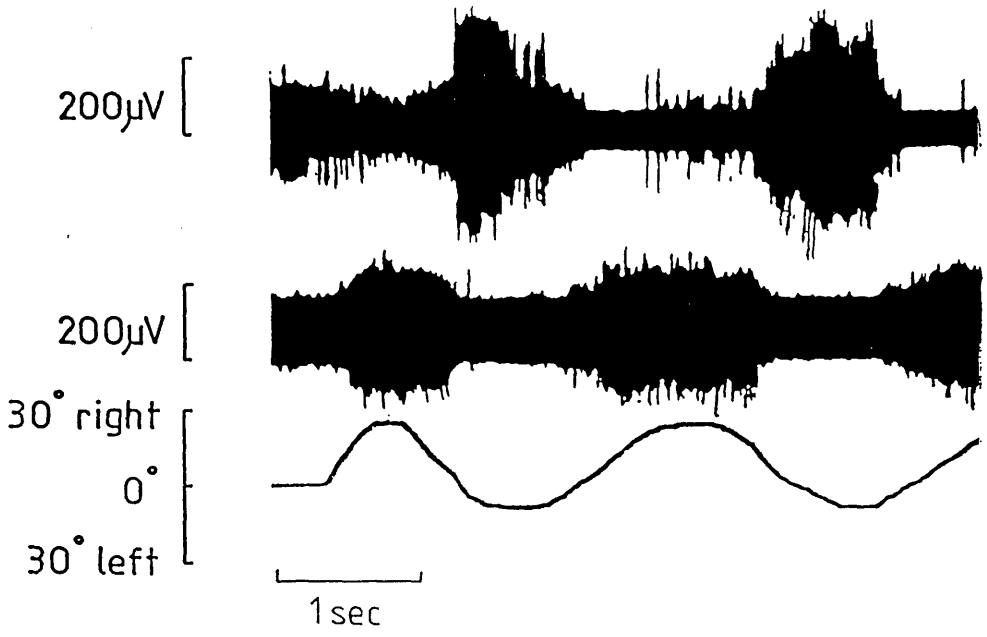


Figure 23. Neck reflex in flexors from opposite forelimbs. EMG activity recorded from the left biceps (upper trace) and right biceps (middle trace) on rotations of the neck (axis vertebra) (lower trace): (decerebrate cat, intact labyrinths, C1 & C2 cut, head fixed in normal position).

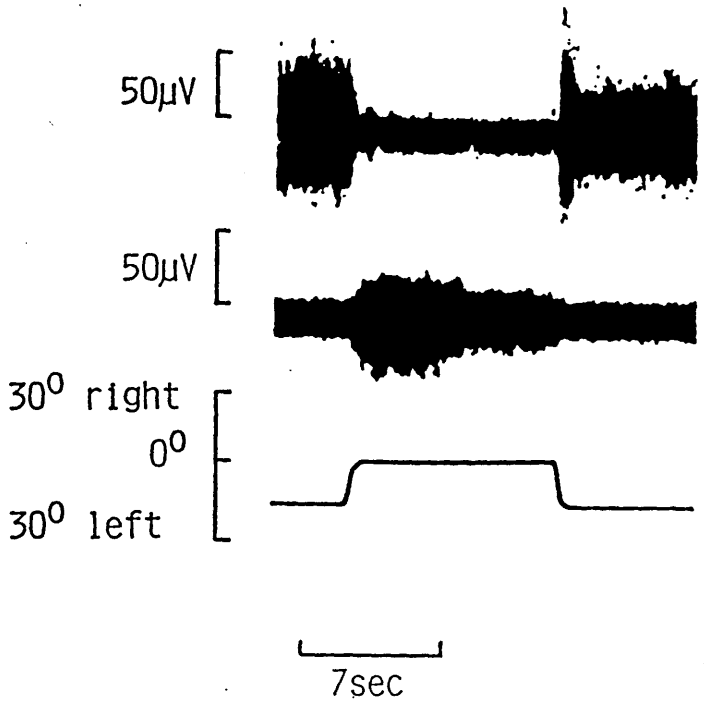


Figure 24. Neck reflex in extensor and flexor of the right forelimb. EMG activity from right triceps (upper trace) and right biceps (middle trace) on rotation of the head toward the right (lower trace): (decerebrate cat, bilateral labyrinthectomy, C1 and C2 intact, axis vertebra clamped).

bilaterally labyrinthectomized cat. This figure illustrates the full pattern of neck reflexes in the right forelimb. The top and middle EMG traces represent the right triceps and biceps respectively, the lower trace, in this figure representing head position. The figure clearly shows the reciprocal nature of neck reflexes acting on triceps and biceps from the same limb. The head rotation to the right leading to a decrease in EMG activity in the right triceps and an increase in the EMG activity of the flexor.

Further to illustrating the pattern of neck reflex action on forelimb muscles from one limb Fig. 24 also serves to illustrate, by comparison with Figs. 17-23 the qualitative similarities between neck reflexes evoked by different methods of activation. In Fig. 24 neck reflexes result from head rotation in a labyrinthless cat. By comparing with response shown in Fig. 17b with that of the extensor in Fig. 24 (top trace) and also Fig. 21a with the flexor of Fig. 24 (middle trace) it can be seen that despite different methods of neck reflex activation the reflex output is the same.

In summary neck reflexes act reciprocally on forelimb extensors (triceps) and flexors (biceps and brachialis) within the same limb. This relationship results in synchronous extension and flexion in opposite limbs on stimulating neck reflex centres. Flexion occurs when the neck is rotated towards a limb and extension when the rotation is directed away from the limb in question.

Neck reflex: side-down tilt = Flexion

side-up tilt = Extension

The complete pattern of neck reflexes for extensor and flexors of both right and left forelimbs is presented in table II for rotations to the right and to the left. The direction of the arrows indicate the direction of EMG activity change.

3.1.9 The antagonism between labyrinth and neck reflexes.

In the previous sections dealing with labyrinth and neck reflexes the behaviour of forelimb muscles during natural stimulation of these reflex systems has been outlined. These reflexes are antagonistic to one another in that on moving the head relative to the body the resultant labyrinth and neck reflexes tend to operate in opposition to each other. This is true for both extensors and flexors.

To illustrate this opposition between the two reflex systems during lateral head tilts a comparison should be made between Fig. 15b and Fig. 24. In both these figures a head rotation to the right acts as the natural stimulus. In Fig. 15b this stimulus results in a labyrinth reflex developing in the extensor and flexor of the right limb, (the axis vertebra is clamped in this example and C1 and C2 have been sectioned). While in Fig. 24 an equivalent head movement in a labyrinthless cat results in neck reflex activity in the right extensor and flexor. Taken together Figs. 15b and 24 provide a comparison of labyrinth and neck reflexes and clearly illustrate that within the forelimbs

	Normal			
	Right limb		Left limb	
	Extensor	Flexor	Extensor	Flexor
Neck rotation to right	↓	↑	↑	↓
Neck rotation to left	↑	↓	↓	↑

Table II. Summary of effects produced by rotations of the neck on the EMG activity of elbow extensors and flexors in cats with intact labyrinths. The arrows indicate increased or decreased activity.

these reflexes act in the opposite direction on triceps and biceps following a rotation of the head about an anterior-posterior axis. The antagonistic relationship between labyrinth and neck reflexes is evident in the musculature of both forelimbs. Tables I and II, which summarize labyrinth and neck reflexes respectively, also illustrate the antagonism between the two reflex systems. Although previously demonstrated in extensor muscles of the forelimb (Lindsay et al., 1976) the antagonism is now also demonstrated to be present in the flexor musculature.

3.1.10 Reflex variations with the condition of the preparation.

Decerebrate rigidity is known to undergo fluctuations in intensity with time (Bazet and Penfield, 1922). It is therefore not surprising that labyrinth and neck reflexes, which act to alter musculature tone, also show considerable variation in efficacy with time, and that these variations may be a function of these fluctuations. During the course of an experiment it was found that in animals showing intense extensor rigidity labyrinth and neck reflexes were only observable in the extensors of the forelimbs, and that these reflexes were small in comparison to the level of background EMG. In the most extreme cases of extensor rigidity no reflexes were observed with head tilt. Recording from flexor muscles in these instances seldom revealed spontaneous EMG activity, (perhaps due to strong reciprocal inhibition from the extensors), and were

never seen to show a response to a head or neck movement. With less intense levels of extensor rigidity the modulation of extensor EMG in terms of signal to noise ratio with head and neck movements became more pronounced. Rotations were seen to suppress or facilitate background EMG levels. As the level of rigidity became less pronounced it was noted that modulation of spontaneous or background flexor EMG activity could be easily observed in addition to that of the extensor muscles studied. In many instances flexor activity was very low but despite this the action of head or neck rotation on the level of EMG activity could be ascertained.

In cases of weak extensor activity it was noticed that flexor activity was either raised or was itself weak. When a period of raised flexor activity accompanied weak extensor EMG it was found that passive movement of a limb from a flexed position to an extended position met with considerable resistance. Head or neck rotations during such circumstances seldom influenced activity levels in extensor muscles, although the flexors showed clear signs of modulated activity. The nature of the distribution and appearance of muscle tone during such periods is reminiscent of previous descriptions of flexor rigidity (Beritoff, 1914: Bazet and Penfield, 1922). Interestingly, the presence of flexor reflex responses to changes in head or neck position without concominant extensor reflex alterations is indicative that the responses observed in flexors are the result of specific labyrinthine or neck afference to flexor motoneurones and not due to segmental

modulation via peripheral loops utilizing reciprocal inhibitory pathways.

During periods where both extensor and flexor activity was weak, the reflex response to head or neck tilt was either very small or absent. As experiments progressed such states would also coincide with a depression of all reflex responses. This reduction in excitability, evident as an inability to evoke withdrawal reflexes, pinna reflexes or coroneal reflexes was a state often from which the preparation would not recover. Spontaneous breathing ceasing shortly (from one half to one hour) after the cat fell into this state. As such, the loss of all reflex responses in cats was taken as a sign of deterioration in the preparation. Spontaneous breathing was prefered to artifical respiration in all experiments on the simple grounds that as the centres responsible for respiration lie in the brain stem (an area of vital importance for the generation of labyrinth reflexes), that disturbances within the breathing pattern could be used as a guide to the viability of the brain stem itself, something that could not be done from artificial respiration.

Although a depression in extensor and flexor activity accompanied the deterioration of the animal there were also times where this reduced background activity did not reflect such a deterioration. In such instances the animal still showed reflex reactions to touching the eyes, the pinna or pinching the toes etc., but not to, or very rarely, to rotations of the neck or head. Labyrinthine and neck reflex could still be observed, albeit indirectly by

conditioning ipsilateral flexion and crossed extensor reflexes with changes in head or neck position. An example of the effect of such conditioning is shown in Fig. 25 where simultaneously recorded ipsilateral flexion and crossed extensor reflexes are compared at different head positions in the response to a fixed stimuli to the right radial nerve. It is clear that the labyrinth can modulate these reflexes recorded from right biceps and left triceps and that the direction of modulation is consistent with labyrinth reflexes recorded in response to a positional change directly. Cats showing this modulation of spinal reflexes by changes in head or in neck position were normally stable in this condition for several hours, after which activity would be re-established and motor responses to changes in head or neck position recorded as normal. During the time an individual cat showed such depressed activity the opportunity was taken to test how changes in limb position affected this modulation of spinal reflexes with changes in head or neck position (the results from these tests are given in a later section, 3.5.0).

3.2.0 The pattern of labyrinth and neck reflexes in acutely hemilabyrinthectomized cats.

Tables I and II provide a summary of the reflex reactions of forelimb extensors and flexors following rotations of the head or neck in decerebrate cats with intact labyrinths (normals). In this section the reflex reactions of these muscles recorded from cats following acute left hemilabyrinthectomy will be presented. The

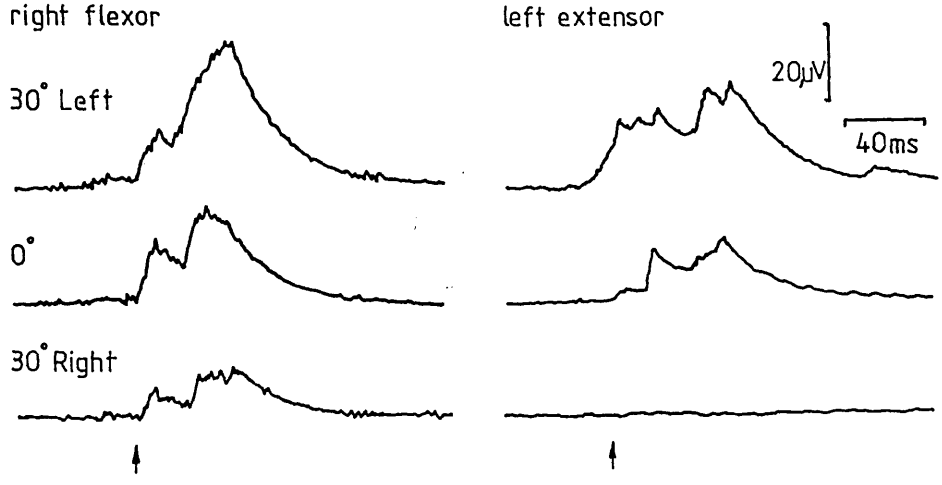


Figure 25. The effect of altering head position on the intensity of simultaneously recorded flexion reflexes in the right biceps and crossed extensor reflexes in the left triceps (illustrated as the rectified and integrated EMG) on electrical stimulation of the dorsal cutaneous branch of the right radial nerve. The stimulus parameters remained constant throughout the series of recordings. Arrows denote the end of the train of stimulus pulses: (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

results of this section are based on 21 successful experiments.

3.2.1 The reactions of extensors to head rotation in acute hemilabyrinthectomized cats.

Following a lateral head tilt Nagaki (1967) and Lindsay and Rosenberg (1978) reported a reversal of the tonic labyrinth reflex following hemilabyrinthectomy in the limb contralateral to the lesion. This observation on the behaviour of the forelimb extensors is confirmed by EMG recordings made in the experiments detailed below.

In all acute experiments labyrinthectomy results in an uneven distribution of decerebrate rigidity. Extensor rigidity ipsilateral to the lesion was practically abolished, with the flexor muscles of that side showing a high degree of activity. Contralateral to the lesion the extensor rigidity was greatly enhanced while the flexors on this side showed little or no spontaneous activity.

EMG recordings from the left triceps during head rotations revealed that the reflex response of this muscle following left hemilabyrinthectomy is in the same direction as that recorded in cats with intact labyrinths. The normal appearance of the labyrinth reflex in the left triceps (medial head) is shown in Fig. 26a and Fig. 26b. Fig. 26 shows that following lateral tilts of the head to the left (Fig. 26a) there is a facilitation of EMG while tilts to the right (Fig. 26b) result in a suppression of EMG. A characteristic feature of these responses, as with that

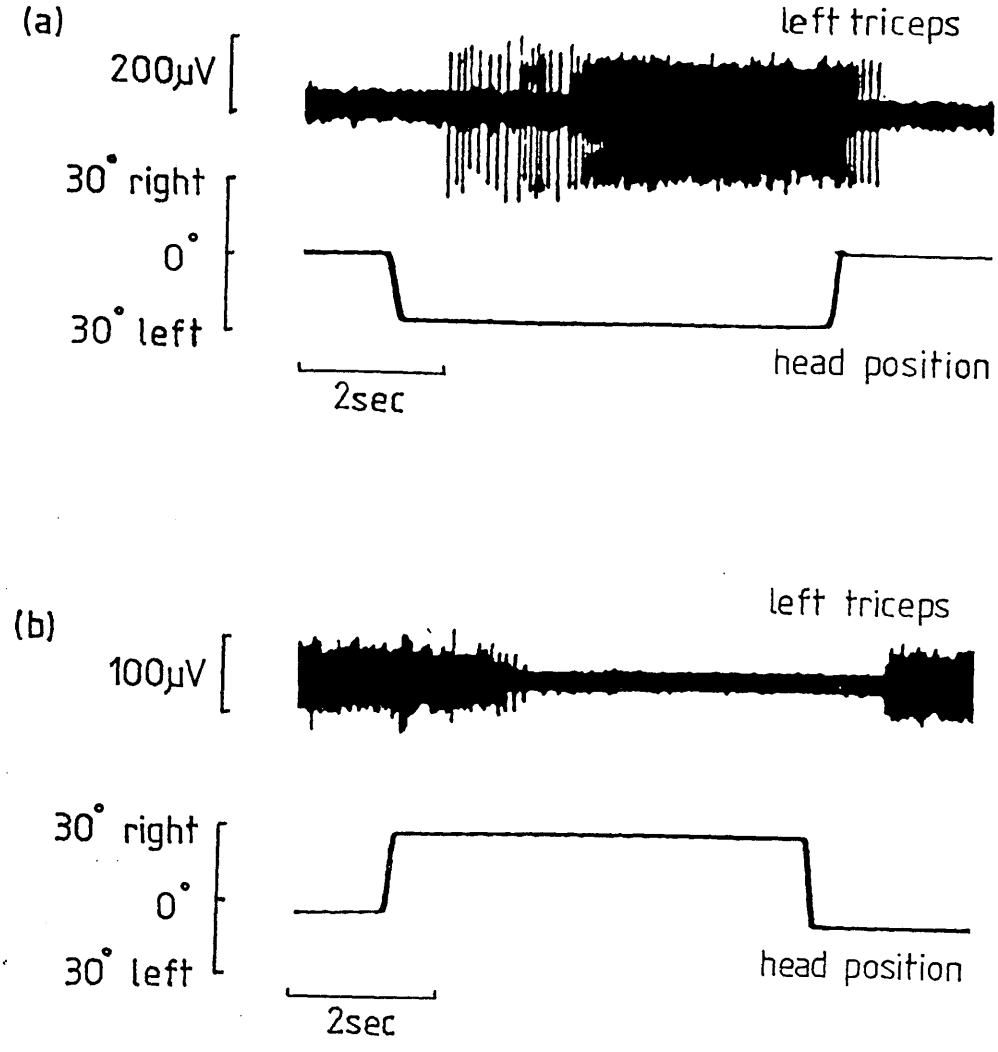


Figure 26. Normal form of labyrinth reflex in left extensor of an acute hemilabyrinthectomized cat. (a) & (b) EMG from left triceps (upper trace) on rotation of the head to the left (lower trace (a)) and to the right (lower trace (b)): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

observed in normal preparations, is the long and variable latency of the reaction to head tilt, and that the activity changes come on slowly to attain a tonic level of activity, which is maintained until the head is returned to the normal position. The increased EMG activity in Fig. 26a on rotation of the head to the left (side-down), results from the recruitment of previously silent motor units, which additionally accelerate output before being silenced on returning the head to the normal position. Fig. 26b illustrates the response of the left triceps to a head tilt toward the right (side-up), and shows that the suppression of activity results from the silencing of previously active motor units. The units become reactivated following the return of the head to the normal position.

The long latencies observed in the responses of Fig. 26a and Fig. 26b are commonly encountered in both normal and acute preparations. The variability in the latency observed in acute animals however, although not systematically examined, seemed to be greater than that in normal cats. Latencies in the acute preparations tending to be greater than those of normals, though short latencies were also frequently encountered. Fig. 27 provides an example of a short latency response. In this figure the integrated EMG from the left triceps is shown on rotation of the head to the left. The response, an increase in EMG activity closely follows the positional change. As mentioned previously, the population of motor units contributing to the reflex will exhibit a distribution of latencies, therefore it becomes difficult to be confident

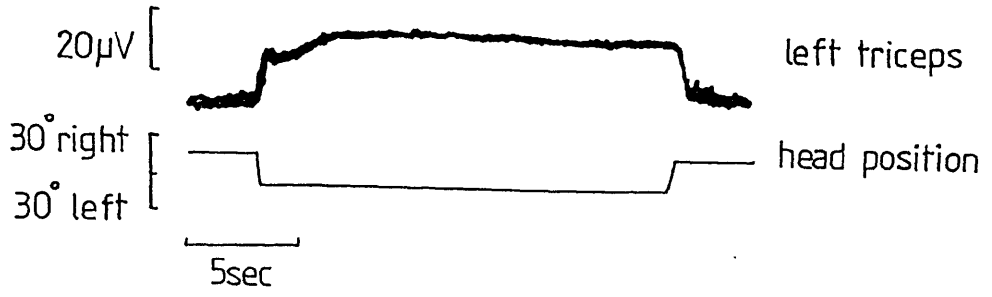


Figure 27. Normal form of labyrinth reflex in an extensor muscle of the left side in an acute hemilabyrinthectomized cat. Rectified and integrated EMG recorded from the left triceps (upper trace) on rotation of the head (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

that experimentally observed latencies reflect the first signs of true reflex activity. Despite this, the latency of any one response can indicate the point whereby certain motor units may be recruited or when the synaptic drive becomes sufficient to accelerate their discharge.

Figs. 26 and 27 show that in the left triceps the normal form of labyrinth reflexes are apparent despite the loss of the ipsilateral labyrinth. The muscle develops tension when the head is tilted to the left and relaxes with head tilts directed toward the right.

As previously mentioned a well documented consequence of hemilabyrinthectomy is that extensor rigidity develops unevenly between left and right limbs. Rigidity, ipsilateral to the lesion being less than that of the intact side. In the experiments reported here this was manifest as weak levels of spontaneous EMG activity in the left triceps. In consequence, head tilts to the right would often fail to produce any evidence of reflex activity, (a not unexpected result, as this direction of tilt tends to suppress EMG activity in this muscle), though rotation of the head to the left, in all but four cats produced typical increases in left extensor activity. In these four cats the EMG from the left triceps never showed any spontantaneous activity, the muscles remaining flaccid throughout the experiment. (It may be that in these examples the loss of facilitatory drive from the ipsilateral vestibulospinal system has been so great that the contralateral labyrinth never succeeds in providing enough drive to sufficiently excite the motoneurone pools.) Despite these failures to

observe a response, the majority of animals during the course of an experiment, would show a response to head tilt in the left limb. These responses were consistent with those depicted in Figs. 26 and 27.

As described above the behaviour of the left triceps muscle group in acute left hemilabyrinthectomized cats is qualitatively identical to the behaviour seen in normal cats. The reflex pattern seen in the right triceps is however not the same as that described for normal animals (see section 3.1.2).

Fig. 28 illustrates the behaviour of the right triceps following a head rotation to the right (Fig. 28a) and a head rotation to the left (Fig. 28b). This figure illustrates that following left hemilabyrinthectomy the reflex response to head tilt in the right extensor is reversed when compared with the response of this muscle seen in cats with intact labyrinths. The right triceps in left hemilabyrinthectomized cats behaving synergistically with the left extensor. Head tilts to the right suppressing the EMG in right (Fig. 28a) and left (Fig. 26b) triceps while facilitation of EMG activity occurs with head tilts to the left (see Fig. 26a:left triceps, Fig. 28b:right triceps). The reversal in the behaviour of the right triceps muscle can be seen by comparing the responses depicted in this Fig. 28 with those from the right triceps taken from cats with intact labyrinths (Figs. 6, 7 and 8). Four further examples of this reflex reversal are given in Fig. 29.

The rectified and integrated EMGs illustrated in

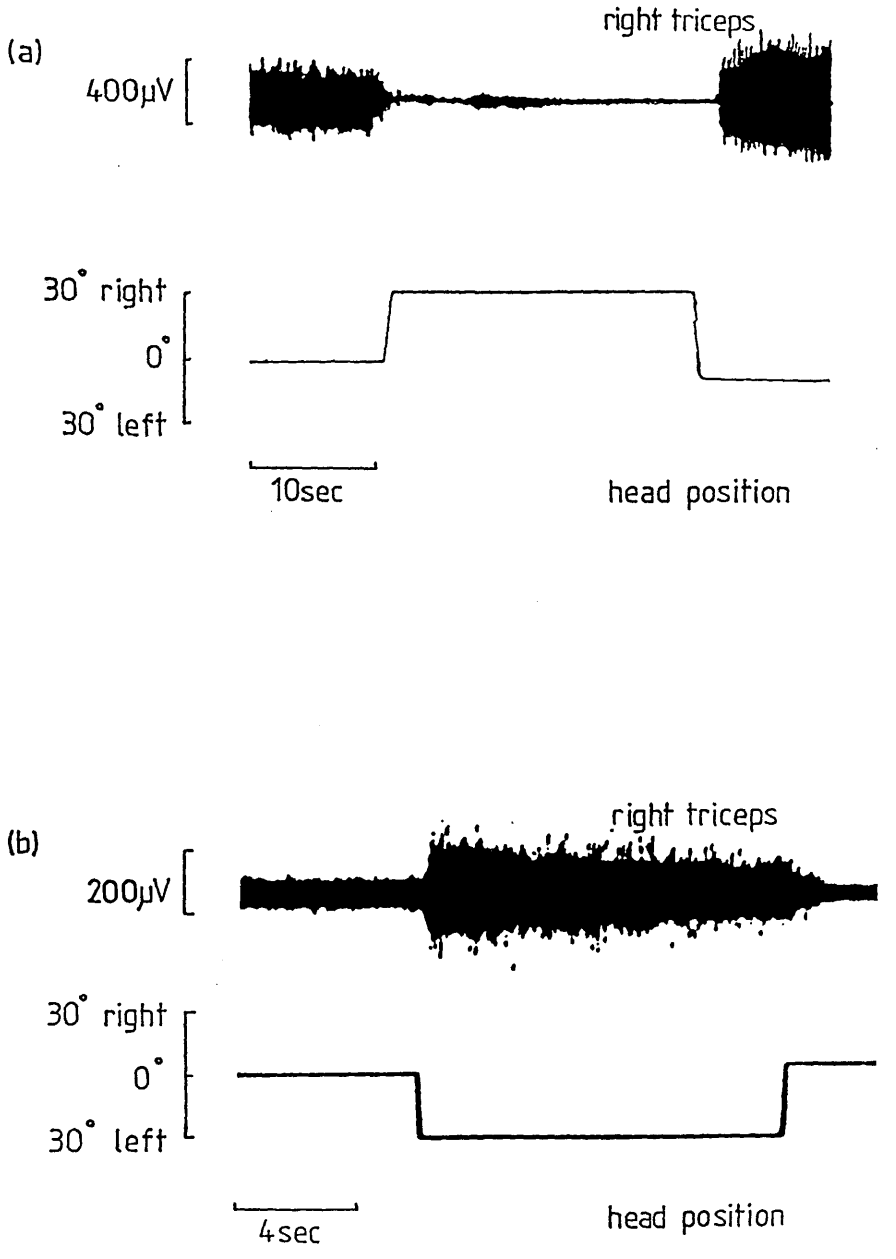


Figure 28. Reversed labyrinth reflex in the right triceps following destruction of the left labyrinth. (a) & (b) EMG from right triceps (upper trace) on rotation of the head to the right (lower trace (a)) and to the left (lower trace (b)): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra cut).

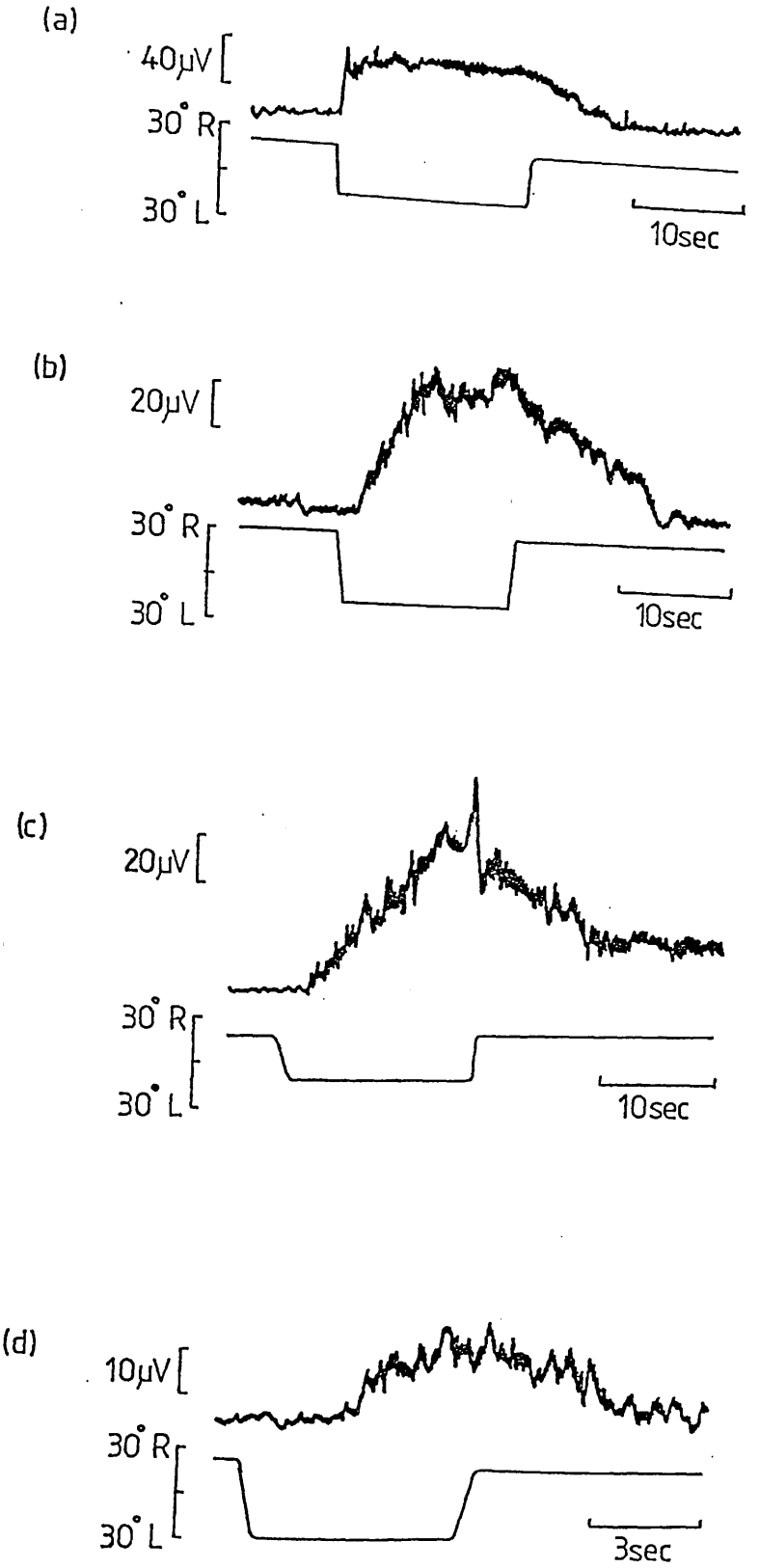


Figure 29. Reversed labyrinth reflex in an extensor muscle of the right side in an acute hemilabyrinthectomized cat. (a), (b), (c) & (d) Different forms of labyrinth reflex illustrated by the rectified and integrated EMG recorded from right triceps on rotation of the head: (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

Fig. 29a,b,c,d show the reflex response of right triceps to head rotations to the left. All examples shown in Fig. 29 illustrate the increase in activity that occurs with this direction of head tilt, and although they share a common direction of response, each example illustrates a different shape of reflex. Fig. 29a shows a response that is almost immediately switched on following the head tilt and exhibits clear tonic activity that correlates with the head tilt. In Fig. 29b and 29c head tilts to the left again produce increases in the EMG from right triceps, although in these cases the integrated EMG slowly increases following head deviation. The response in Fig. 29b eventually reaches a plateau that is maintained for the duration of the tilt before gradually returning toward previous resting EMG levels on completion of the head tilt. Although the response in Fig. 29c is similar it does not reach a maintained plateau level during the tilt, as the head is returned to the normal position prior to this being achieved. As the tilt lasts approximately 18 seconds it would seem that the muscle throughout this period of time is becoming progressively more active. On returning the head to the normal position there is a slow decline in the integrated EMG. A different response pattern is shown in Fig. 29d. Here the integrated EMG again shows an increased activity though only after a considerable delay (approx' 2.5sec), following which a maintained increase is seen which in total time corresponds closely with the length of time the head is held in the left side-down position. The complete response taking on the appearance of being time

shifted (lagging) with respect to the stimulus.

The examples of activity changes observed in Fig. 29 correlate well with the positonal change, although the shapes of the responses do not always reflect the shape of the positional change. Whereas in normal preparations a phasic increase can occasionally be recognised along with a tonic component, it is difficult in these examples to match a steady increase in activity (Fig. 29c) with what in terms of otolith output should be a steady signal. In these examples it would seem that these increases reflect successive recruitment of higher threshold motor units during the tilt and that the slow decline is also a consequence of this, in that the less excitable fibres will drop out earlier than the more excitable ones. From these figures of activity in the right triceps the only truly consistent observation is the direction of the activity changes. Rotations to the left increasing EMG, while rotations to the right tend to suppress the electrical activity of the right extensor.

The behaviour of the EMG from forelimb extensors during lateral head tilts in acute left hemilabyrinthectomized cat are consistent with previous reports of labyrinth positional reflexes in such preparations (Nagaki, 1967; Lindsay and Rosenberg, 1978). The direction of the reflex in the left limb remaining unaltered while that in the right limb is reversed. This giving rise to coactivation of left and right extensor muscles following tilts to the left and a simultaneous depression of EMG activity with rotations to the right.

3.2.2 The flexor motor response to changes in head position and the relationship between flexor and extensor activity in acute left hemilabyrinthectomized cats.

Head tilts, as has previously been described, affect the motor output of flexor muscles of the forelimb. In this section the pattern of flexor muscle behaviour during head tilts in the decerebrate cat following acute left hemilabyrinthectomy will be described. In all the experiments reported in this section neck reflexes were excluded by clamping the axis vertebra after sectioning C1 and C2.

In a cat with intact labyrinths head tilts result in activation of forelimb flexors (biceps and brachialis) when the direction of tilt is directed away from the recording site (ie. side-up tilts, with side-down tilts depressing flexor EMG). Following left labyrinthectomy this situation is altered. The results to be presented which describe the flexor pattern in acute animals are based on information obtained from 19 cats. Of this group 16 showed consistent changes in flexor activity with head tilt while in 3 animals an alternative pattern was observed. The pattern of labyrinth reflexes observed in the majority of the animals will be described first, that from the remaining 3 will be dealt with separately.

Rotations of the head in the majority of experiments resulted in labyrinth reflexes in the left flexors (biceps and brachialis) that are consistent with

those recorded from cats with intact labyrinths. That is, rotation of the head to the left depressed EMG activity while increases in EMG accompany head rotations toward the right. Fig. 30 shows the integrated EMG recorded from the left brachialis during a head tilt to the left. The figure illustrates a tonic suppression of EMG activity accompanying the head tilt, furthermore when the tilt is directed to the right (as illustrated in the raw EMG recording from left biceps in Fig. 31) the result is a tonic increase in motor output. Such behaviour is depicted in Fig. 32 which shows the EMG response of the left biceps to successive tilts of the head to the right. In this figure it can be seen that the periods of increased EMG activity correspond with periods when the head occupies a right side-down attitude. Together Figs. 30, 31 and 32 show the typical form of the labyrinth reflex recorded in the left flexor following unilateral destruction of the left labyrinth. The reflex response of these muscles during head rotation is equivalent to the reflex behaviour of the same muscle group in cats with intact labyrinths, as described in a previous section (3.1.3).

Although the reflex output recorded in the left flexor muscles appear, qualitatively, unaltered following left labyrinthectomy the response of the right flexor (like that of the right extensor) is different from the response seen in the normal case.

The behaviour of the right forelimb flexors biceps and brachialis are illustrated in the following figures. Fig. 33 depicts the activity changes in the integrated EMG

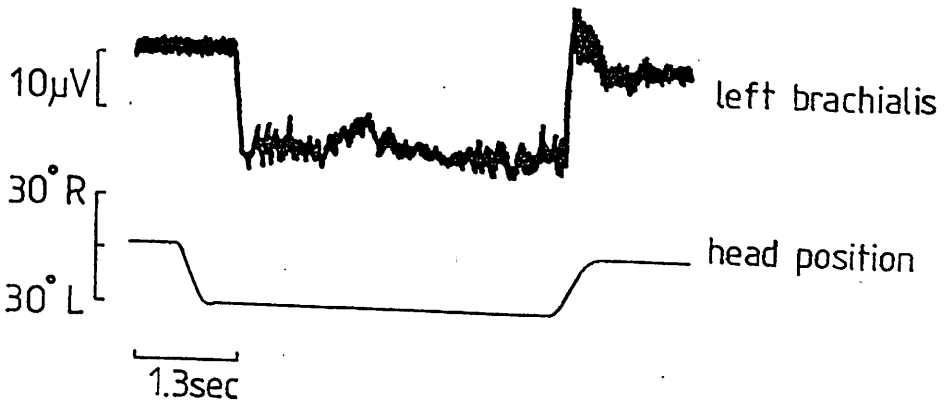


Figure 30. Normal labyrinth reflex in a flexor muscle of the left side in an acute hemilabyrinthectomized cat. Rectified and integrated EMG recorded from the left brachialis (upper trace) on rotation of the head (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

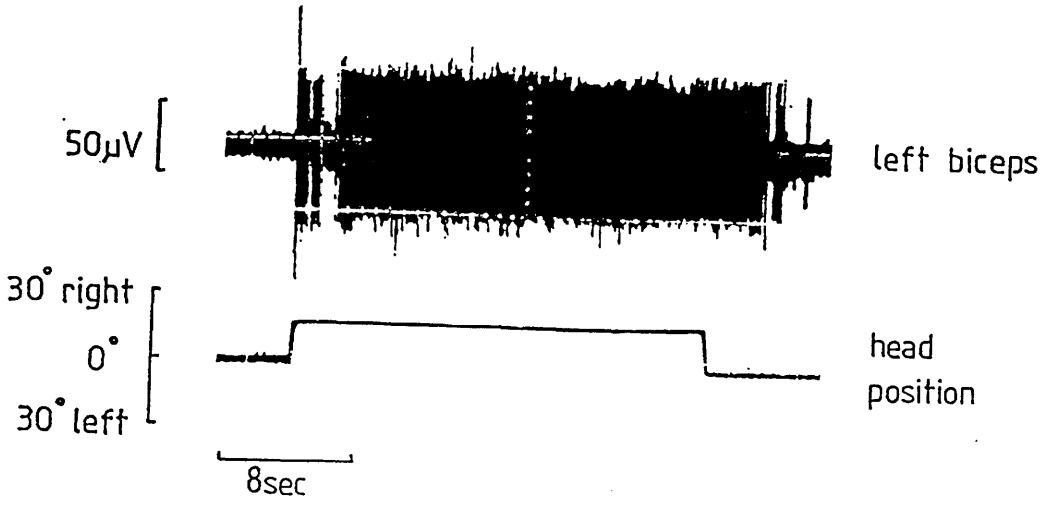


Figure 31. Normal labyrinth reflex in a flexor muscle of the left side in an acute hemilabyrinthectomized cat. EMG from left biceps (upper trace) on rotation of the head to the right (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

Figure 32. Normal labyrinth reflex in left biceps in an acute hemilabyrinthectomized cat. EMG from left biceps (upper trace) on rotation of the head (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

Figure 33. Reversed labyrinth reflex in a flexor of the right forelimb in an acute hemilabyrinthectomized cat. Rectified and integrated EMG from the right biceps (upper trace) on rotation of the head to the left (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

of the right biceps following rotation of the head to the left. Ordinarily in the normal decerebrate preparation such a tilt is associated with an increase in the motor output of the right biceps, however in this figure such a tilt is correlated with a depression in motor activity. The depression, typically, persists until the head is rotated back toward the starting position, following which (after a delay) EMG is re-established near to pre-tilt levels. When the direction of the tilt is toward the right the EMG responds with an increase in activity. Examples of the EMG response to head rotations toward the right side of the animal are shown in Figs. 34 and 35. In Fig. 34 the rectified and integrated EMG from the right biceps is illustrated and in Fig. 35 the EMG recorded from the right brachialis is shown. Both examples illustrate the response for the same direction of head rotation (to the right) and each show associated increases in motor output. Furthermore, these responses are maintaned at elevated activity levels until the head is returned to its original position. The behaviour of right biceps and brachialis in Figs. 33, 34 and 35, in acute left hemilabyrinthectomized preparations illustrate that the reflex response to lateral head tilts is reversed in comparison to the normal reflex action observed in these muscles in cats with intact labyrinths (see Figs. 10, 11b, 15b).

In consequence to this reversal in activity pattern, as observed in the right flexor muscles, head tilts which previously resulted in reciprocal activity changes in flexors from left and right forelimbs result in

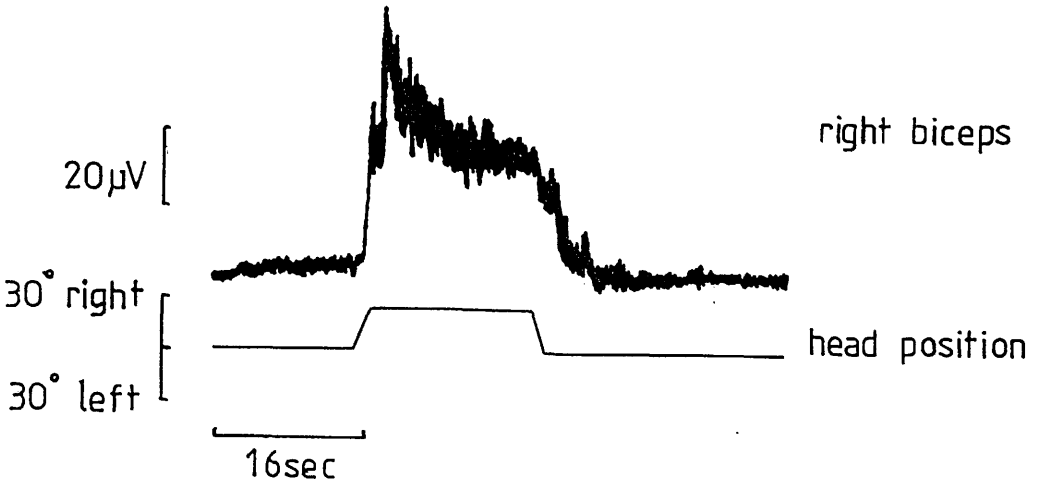


Figure 34. Reversed labyrinth reflex seen in right biceps of an acutely hemilabyrinthectomized cat. Rectified and integrated EMG from the right biceps (upper trace) on rotation of the head to the right (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

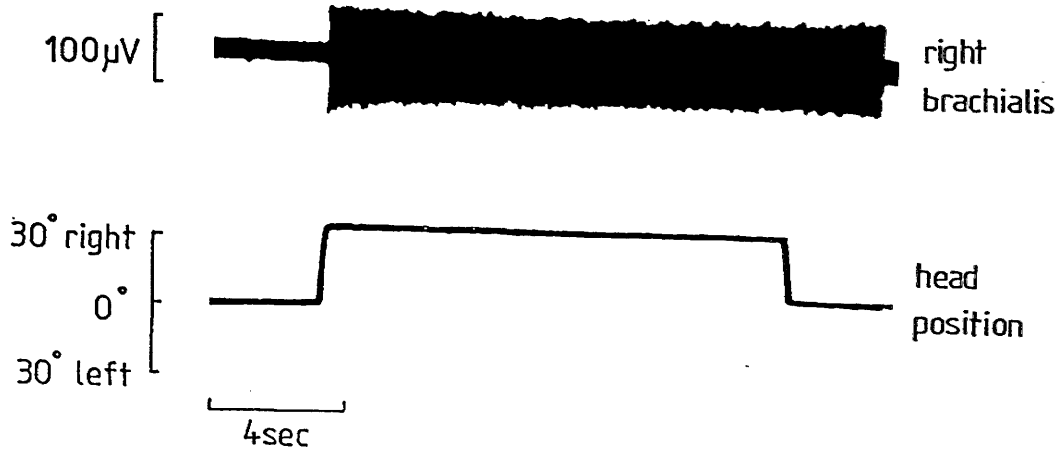


Figure 35. Reversed labyrinth reflex seen in right brachialis of an acutely hemilabyrinthectomized cat. EMG recorded from the right brachialis (upper trace) on rotation of the head to the right (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

a coactivation or suppression in activity after the loss of the left labyrinth. Acute left hemilabyrinthectomy therefore results in right and left flexors becoming synchronously active with head rotations to the right. Two examples of this coactivation of crossed flexors are shown in Fig. 36 (a and b). In both Fig. 36a and 36b the EMG recorded from the right biceps is shown on the top trace and that from the left biceps is represented below this. In Fig. 36b the latency of the response to head tilt is much greater than that observed in Fig. 36a. Interestingly, in both examples latency for left and right flexor muscles are similar. This suggests that despite probable differences in the population of motor unit types being sampled from one muscle, in comparison to another, that latency may be more dependant on central mechanisms rather than on differences in the synaptic drive on to motorneurones supplying different motor units. Despite this speculation, what is clear is that hemilabyrinthectomy, by virtue of a reversed labyrinth reflex contralateral to the lesion alters the relationship between flexor muscles of opposite forelimbs.

As the behaviour of the right extensor is also reversed following destruction of the left labyrinth the intermuscular relationship between right flexor and extensor remains one of reciprocating activity in response to head tilts. Fig. 37 illustrates that this is indeed the case. The rectified and integrated electromyograms of the right triceps (Fig. 37a) and right biceps (Fig. 37b) are shown in response to succesive head tilts. Rotations to the left increase extensor activity and are accompanied by

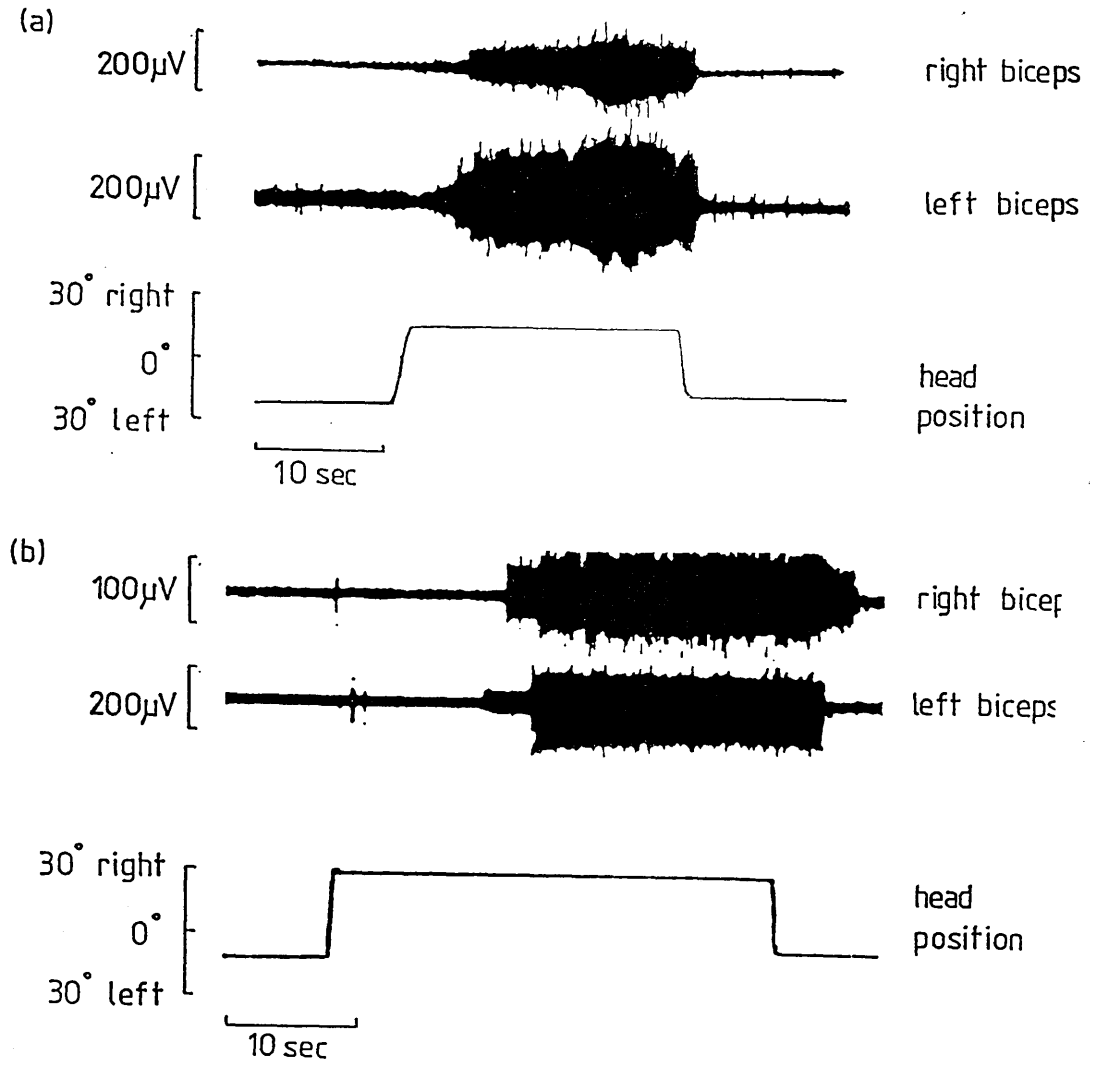


Figure 36. Coactivation of flexor muscles from opposite forelimbs during labyrinthine stimulation in an acutely hemilabyrinthectomized cat. (a) & (b) EMG from right (upper trace) and left (middle trace) biceps on rotation of the head (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

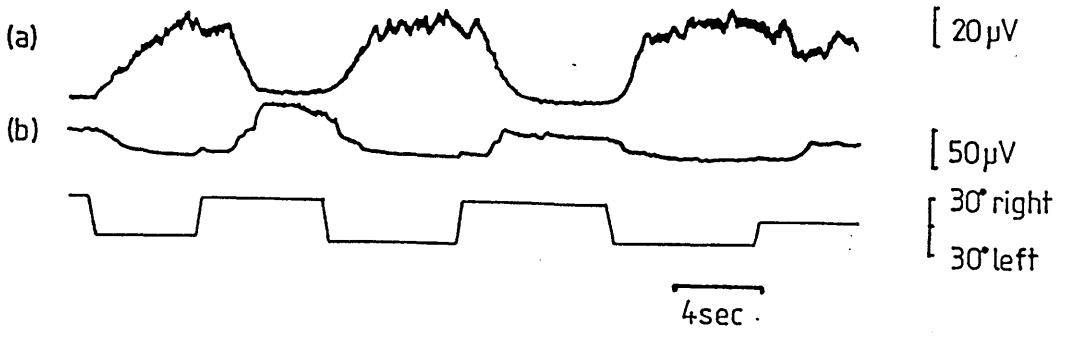


Figure 37. Reversed labyrinth reflex in extensor and flexor of right forelimb, preserving reciprocal reflexes in that limb in the acute hemilabyrinthectomized cat. Rectified and integrated EMG from the right triceps (a), and the right biceps (b) on rotation of the head (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

simultaneous reductions in flexor activity. Similarly when the head is rotated from a left side-down position to a normal position a decreased extensor output is accompanied by an increase in flexor activity. This form of reflex behaviour, due to the reversal of extensor and flexor activities in the right forelimb, is reminisent of the pattern of labyrinthine reflexes in the left limb in normal and left hemilabyrinthectomized cats. In the left limb the normal pattern of reciprocal extensor and flexor activity is observed following a lateral head tilt in the acute preparation. An example illustrating both flexor and extensor activity in the left limb is shown in Fig. 38. This example, in support of previous figures dealing with individual muscles in the left limb and in comparison with Fig. 15a (normal), shows that the direction of the labyrinth reflex is not altered following left labyrinthectomy. Such behaviour within the left limb and in conjunction with that occurring in the right limb, results in the normal asymmetry between the limbs being lost on labyrinthectomy. Thus, rather than having synchronous extension and flexion in opposite limbs, hemilabyrinthectomy results in extensors of one limb showing reciprocal activity with not only flexors of the same side (Figs. 37 and 38) but also with flexors of the opposite limb. Fig. 39 records such crossed reciprocal behaviour in response to a head tilt. The figure shows the response of the right triceps (top trace) and left brachialis (middle trace) following a head rotation from a right side-down position to a left side-down position. The

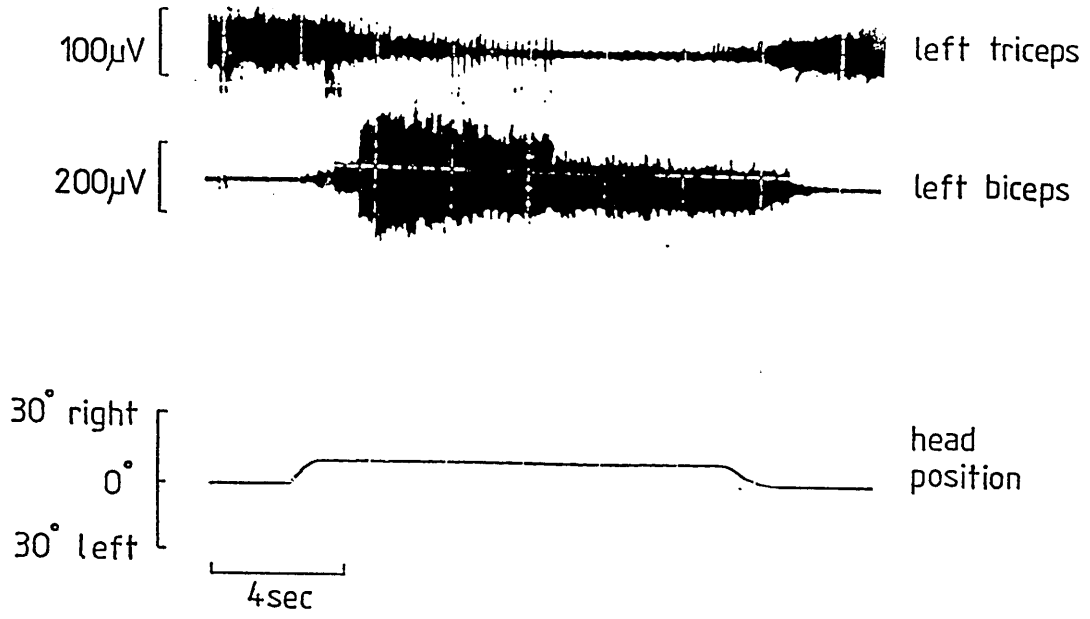


Figure 38. Normal pattern of reciprocal extensor and flexor labyrinth reflexes in the left forelimb of an acutely hemilabyrinthectomized cat. EMG from the left triceps (upper trace) and from the left biceps (middle trace) on rotation of the head (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

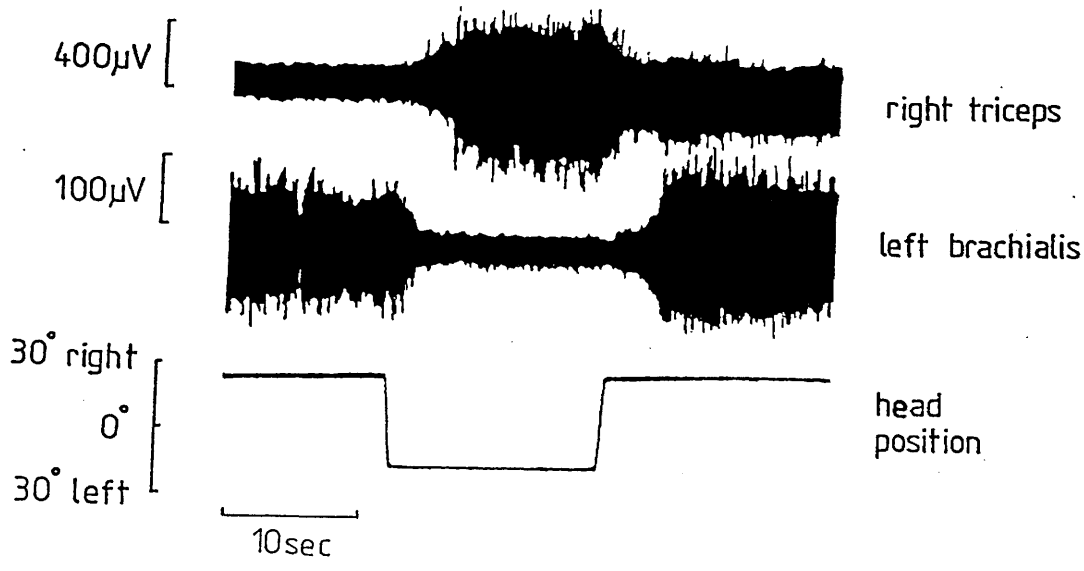


Figure 39. Reciprocal labyrinth reflexes in extensor and flexor from opposite limbs in an acutely hemilabyrinthectomized cat. EMG from the right triceps (upper trace) and left brachialis (middle trace) on rotation of the head (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

figure demonstrates that there is a concominant increase in activity from right triceps and a decrease in left brachialis EMG with the head tilt illustrated.

Left labyrinthectomy therefore can be seen to alter the reflex response to a head tilt by reversing both the extensor and flexor motor outputs of the right limb. This disruption to the normal pattern of reflexes resulting in coactivation of flexors in opposite limbs, when the tilt is directed away from the lesion, and coactivation of opposite extensors when the head tilt is toward the side of the lesion. The pattern of labyrinth reflexes observed in the acute left hemilabyrinthectomized cat is summarised in table III.

This table it should be noted is composed in respect to the majority of responses seen in any one muscle. Deviations in this pattern were seen in three preparations, the disagreeement only occurring in the behaviour of the left flexor. This departure from the common form of the labyrinth reflex will be discussed in a separate section.

It should also be noted that the above reflexes on a subsequent second labyrinthectomy are completely abolished, thus demonstrating there dependance on the integrity of the right labyrinth (a right labyrinthectomy was carried out on 3 cats).

3.2.3 The pattern of neck reflexes in the forelimb muscles of acute left hemilabyrinthectomized cats.

	Acute hemilabyrinthectomy			
	Right limb		Left limb	
	Extensor	Flexor	Extensor	Flexor
Head rotation to right	↓	↑	↓	↑
Head rotation to left	↑	↓	↑	↓

Table III. Summary of effects produced by rotations of the head on the EMG activity of elbow extensors and flexors in acute left hemilabyrinthectomized cats. The arrows indicate increased or decreased activity.

In the previous sections the behaviour of forelimb muscles is shown to change following left labyrinthectomy. In this section the pattern of neck reflexes will be described for this preparation. In all the experiments carried out on acute animals, left labyrinthectomy never altered the pattern of neck reflexes.

As in the normal intact labyrinth preparation rotations of the axis vertebra to side-up positions resulted in tonic increases in the EMG recorded from forelimb extensors. Thus a rotation of the neck to the left results in an increase in right triceps activity (see integrated EMG in Fig. 40) while a rotation of the neck to the right evokes increased EMG from the left triceps (see integrated EMG in Fig. 41). This demonstrating that following unilateral labyrinthectomy the normal reciprocity between forelimb extensors of the left and right sides is maintained. Similarly, the asymmetry in response to tilts of opposite directions within one limb is preserved, this is illustrated in the response of the right triceps to successive neck rotations in Fig. 42. In this figure rotation of the neck to the right results in (as expected) a partial suppression of EMG activity, which lasts until the neck is returned to the mid-position, subsequent rotation of the neck to the left shows the opposite behaviour. With this rotation the right extensor shows a tonic increase in motor output. This type of motor activity is identical to the form of neck reflexes recorded from cats with intact labyrinths and indicates that acute hemilabyrinthectomy does not influence the extensor form of

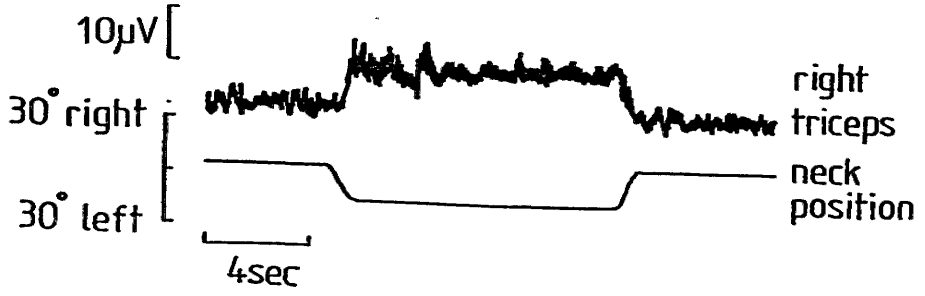


Figure 40. Normal pattern of neck reflex in right extensor muscle of an acutely hemilabyrinthectomized cat. Rectified and integrated EMG from the right triceps (upper trace) on rotation of the axis vertebra to the left (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, head fixed in normal position).

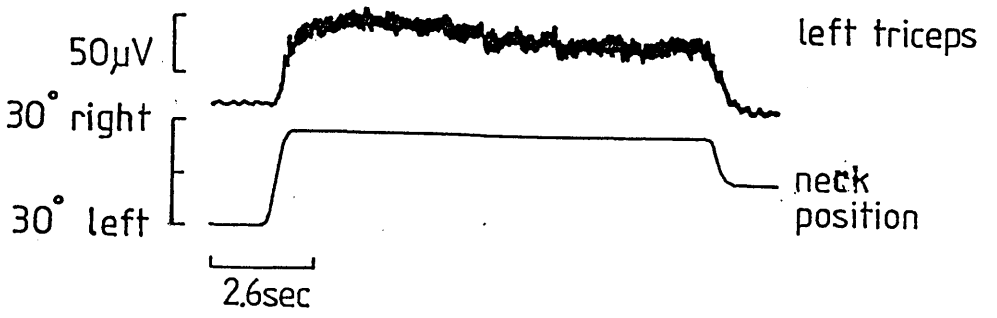


Figure 41. Normal pattern of neck reflex in an extensor of the left forelimb of an acutely hemilabyrinthectomized cat. Rectified and integrated EMG from the left triceps (upper trace) on rotation of the axis vertebra (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, head fixed in normal position).

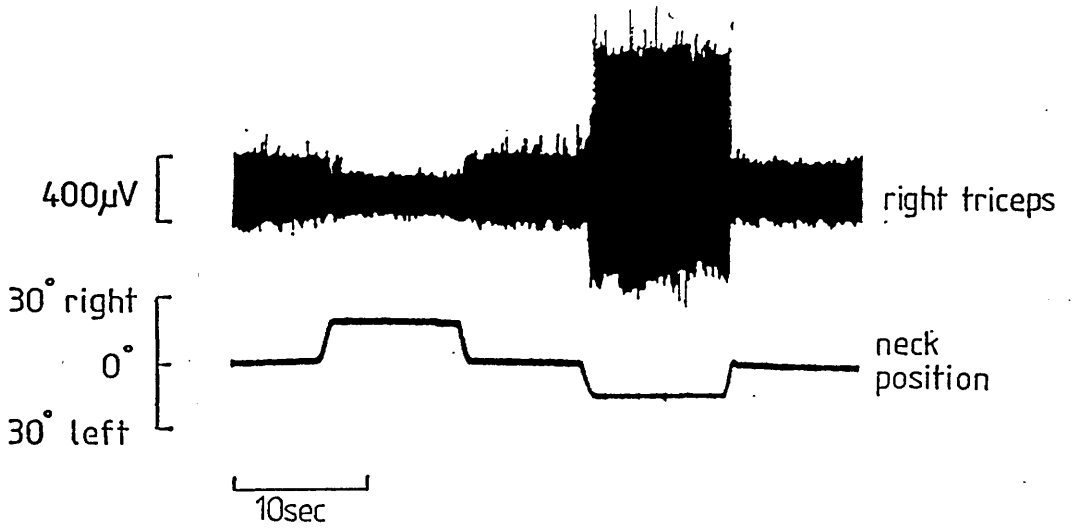


Figure 42. Normal pattern of neck reflex in an extensor of the right forelimb in an acutely hemilabyrinthectomized cat. EMG from the right triceps (upper trace) on rotation of the axis vertebra (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, head fixed in normal position).

the neck reflex.

Just as extensor neck reflexes appear normal so do those recorded from the flexor muscles. This is illustrated in Figs. 43 and 44. In Fig. 43 the integrated EMG of the right biceps is shown following a neck rotation to the left. The consequence of the rotation is a clear depression in activity, as would be expected from the form of normal neck reflexes depicted in table II. Equivalence between neck reflexes in the left biceps in normal and acute preparations is seen by studying the reflex behaviour depicted in Fig. 44. In this example of neck reflex influence on flexor musculature the raw EMG shows a depression of activity with rotations to the right, and an enhancement of motor output when the tilt is directed toward the left side of the animal. Comparisons with responses shown in earlier sections illustrate that this form of reflex behaviour is qualitatively the same in both acute and normal preparations. Thus both flexor and extensor muscles of the same forelimb respond reciprocally to neck rotations in acutely hemilabyrinthectomized animals (see Fig. 45). Consequently rotation of the neck, irrespective of the integrity of the labyrinths can induce extension in one limb and flexion in another, as illustrated in Fig. 46.

The pattern of neck reflexes seen in acutely left hemilabyrinthectomized cats is summarised in table IV. In the normal animal this pattern of activity represents a pattern of reflex actions that oppose reflexes from the labyrinths. However due to the altered labyrinth reflex in

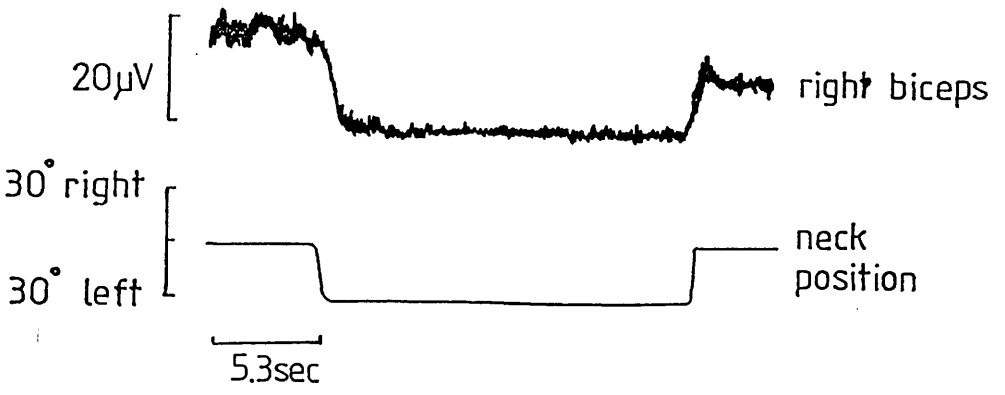


Figure 43. Normal pattern of neck reflex in the right biceps of an acutely hemilabyrinthectomized cat. Rectified and integrated EMG from the right biceps on rotation of the axis vertebra to the left (lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, head fixed in normal position).

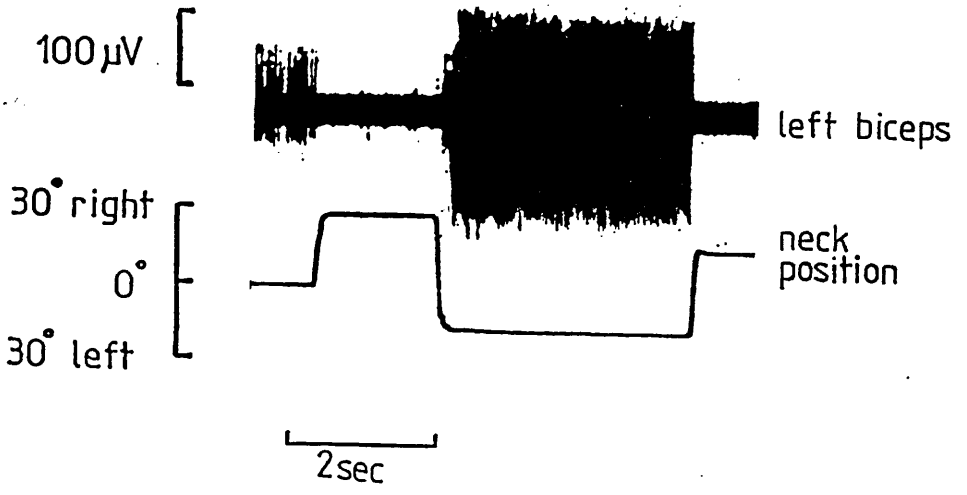


Figure 44. Normal pattern of neck reflex in the left biceps of an acutely hemilabyrinthectomized cat. EMG from the left biceps on rotation of the neck (axis vertebra): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, head fixed in normal position).

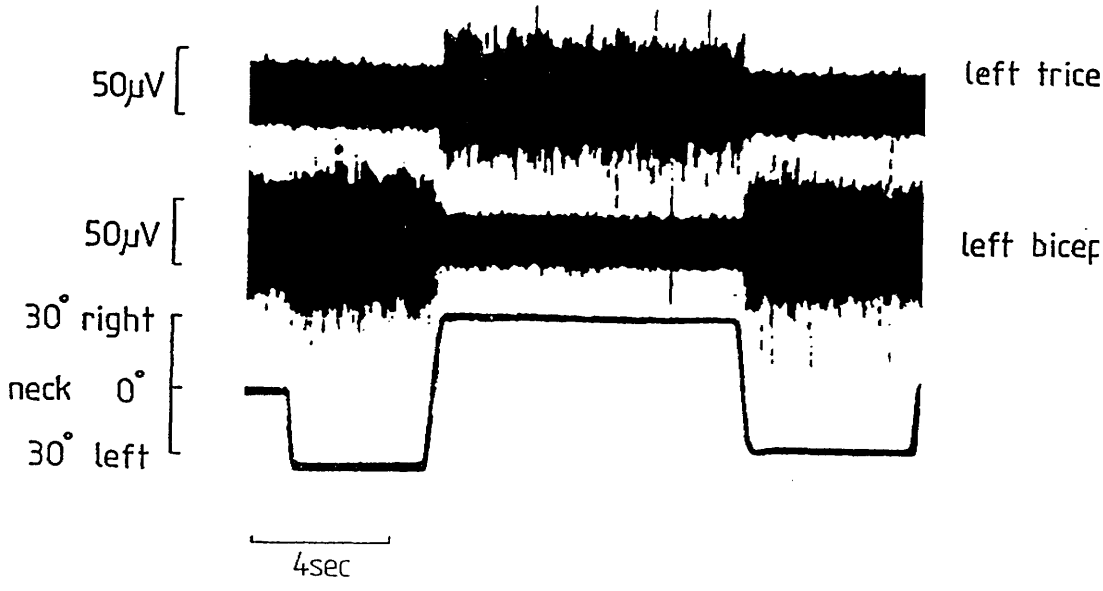


Figure 45. Normal pattern of reciprocal neck reflexes in extensor and flexor muscles of the same limb in an acutely hemilabyrinthectomized cat. EMG from the left triceps (upper trace) and left biceps (middle trace) on rotation of the neck (axis vertebra, lower trace): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, head fixed in normal position).

	Acute hemilabyrinthectomy			
	Right limb		Left limb	
	Extensor	Flexor	Extensor	Flexor
Neck rotation to right	↓	↑	↑	↓
Neck rotation to left	↑	↓	↓	↑

Table IV. Summary of effects produced by rotations of the neck on the EMG activity of elbow extensors and flexors in acute left hemilabyrinthectomized cats. The arrows indicate increased or decreased activity.

the acute preparation this is no longer true and a different pattern of interaction between labyrinth and neck reflexes is seen. The form of the interaction between these reflexes in the acute preparation is given below.

3.2.4 The interaction between labyrinth and neck reflexes in the acute preparation.

In the normal animal, with intact labyrinths, reflexes from the head and neck act in opposition, whereas in the acute animal this situation is altered. In the acute animal the labyrinth reflex ipsilateral to the lesion appears in the same direction as that in the normal animal. As neck reflexes in the acute preparation also appear normal then the interaction between neck and head influences in the limb ipsilateral to the lesion (left side) should appear normal. This antagonism in reflex response resulting from similarly directed rotational movements of the head and neck are shown for the left biceps in Fig. 47. This figure demonstrates the ability of neck and labyrinth reflexes to oppose each other in the left limb following unilateral destruction of the left labyrinth. In Fig. 47a a rotation of the head to the right (lower trace) increases the EMG of the left flexor (upper trace), this labyrinth reflex is however suppressed on subsequent rotation of the neck to the right (middle trace). The increased reflex response reappears on returning the neck to its original position. A similar antagonistic interaction is seen when the rotations are

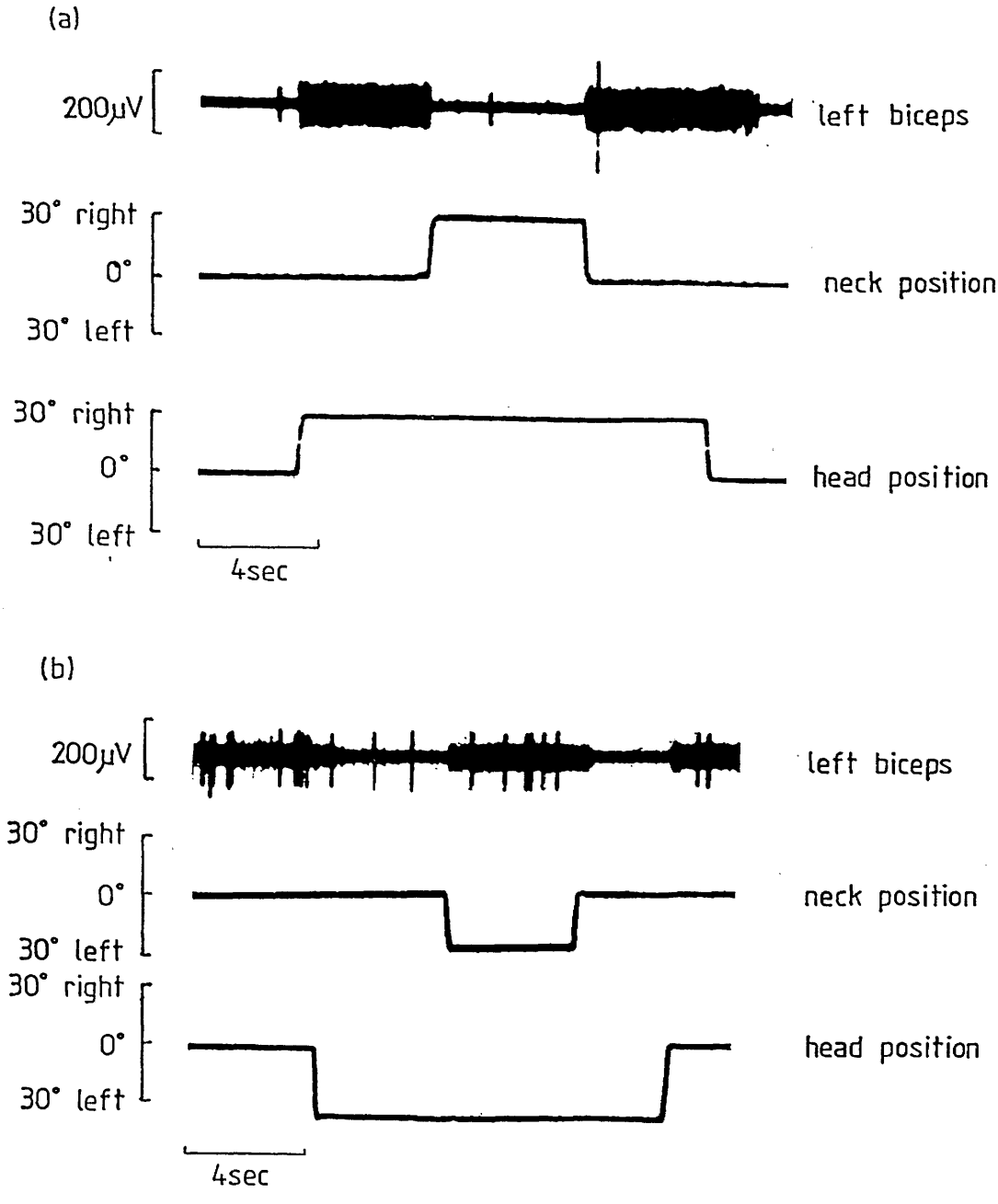


Figure 47. (a) & (b) Normal pattern of interaction of labyrinth and neck reflexes in the left biceps in an acutely hemilabyrinthectomized cat. Neck position is indicated by the middle traces and head position by the lower traces in (a) & (b): (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut).

directed towards the left (Fig. 47b).

In the right limb, that is contralateral to the lesion, the pattern of labyrinth and neck reflex interactions are altered as a result of the labyrinthectomy. With the reversal in the direction of the labyrinth reflex in the right extensor and flexor, neck rotations in the same direction as head tilts result in additive reflexes rather than opposing ones. Fig. 48 illustrates how this alters the interaction of labyrinth and neck reflexes. It can be seen from Fig. 48 that when a labyrinth reflex is superimposed on a pre-existing neck reflex in the right triceps that both influences act in the same manner. The example shows an increase in the rectified and integrated EMG from the extensor resulting from a neck rotation to the left with a further enhancement in activity when the head is tilted in the same direction. The reversed labyrinth reflex can be seen to sit on-top of the pre-existing neck reflex rather than acting to oppose it. A similar form of reflex interaction is seen in the flexors of the right limb. Fig. 49 shows the effect of neck reflex interaction with a reversed labyrinth reflex in the right biceps. In this example the rotations are directed towards the right and it can be seen that, as with the extensor of this limb, there is a summation of reflex influences. The neck reflex with its normal form inducing a further increase in the motor output of this muscle.

In the acute hemilabyrinthectomized cat it can therefore be concluded that ipsilateral to the lesion there are no obvious signs of reflex disturbance, though

Figure 48. Abnormal interaction of labyrinth and neck reflexes in the right triceps (upper trace) of an acutely hemilabyrinthectomized cat. The rectified and integrated EMG is shown along with neck (middle trace) and head (lower trace) position: (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut).

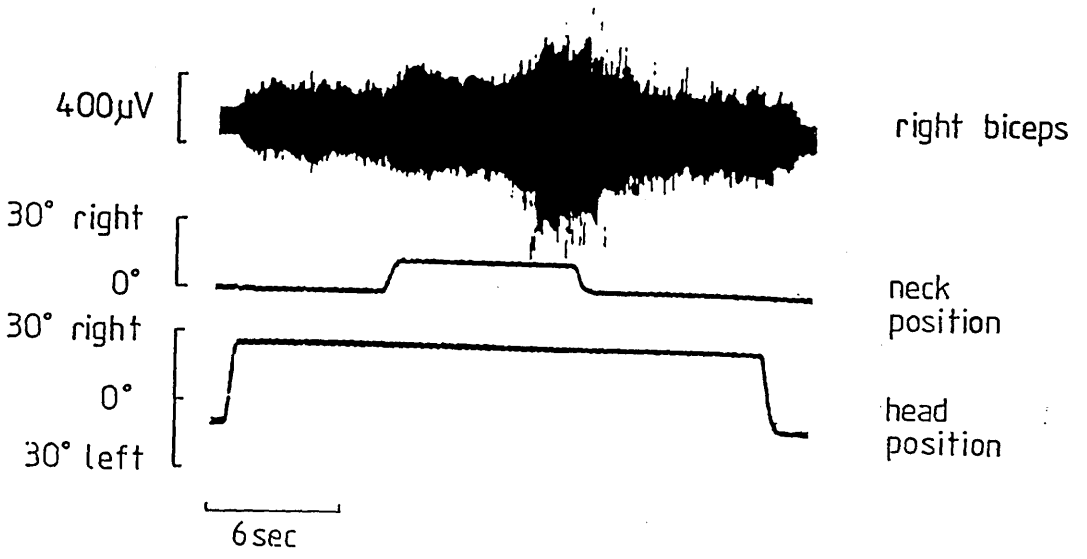


Figure 49. Abnormal interaction of labyrinth and neck reflexes in the right biceps (upper trace) in an acutely hemilabyrinthectomized cat. Neck and head position are represented by middle and lower traces respectively: (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut).

contralateral to the lesion (i.e., the intact side) the labyrinth reflex is reversed and this results in abnormal reflex interactions with neck reflexes. This abnormal reflex interaction would seem a plausible explanation for some of the postural disturbances seen in conscious animals following the loss of one labyrinth.

3.2.5 An alternative response pattern seen in the left flexor in some acute preparations.

As mentioned earlier (section 3.2.2) the behaviour of the left biceps in the majority of cats following left labyrinthectomy was similar to that seen in cats with intact labyrinths. This situation however was not observed in three cats out of the group of acute animals. In these three cats the labyrinth reflex in the left flexors was reversed. Figs. 50 and 51 illustrate the consequence of this reversal in behaviour in terms of the reflex interaction between the labyrinth and neck reflex systems. In Fig. 50 it can be seen that a head rotation to the left results in signs of increased muscle activity, whereas in the previously reported experiments this muscle (left biceps) normally responds with a suppression in EMG. With a rotation of the neck to the left superimposed upon this reversed reflex the resulting neck reflex can be seen to further increase the motor output of the muscle. In this example the neck reflex is added to the reversed labyrinth reflex. Similar behaviour is illustrated in Fig. 51 where a labyrinthine reflex is shown superimposed upon a

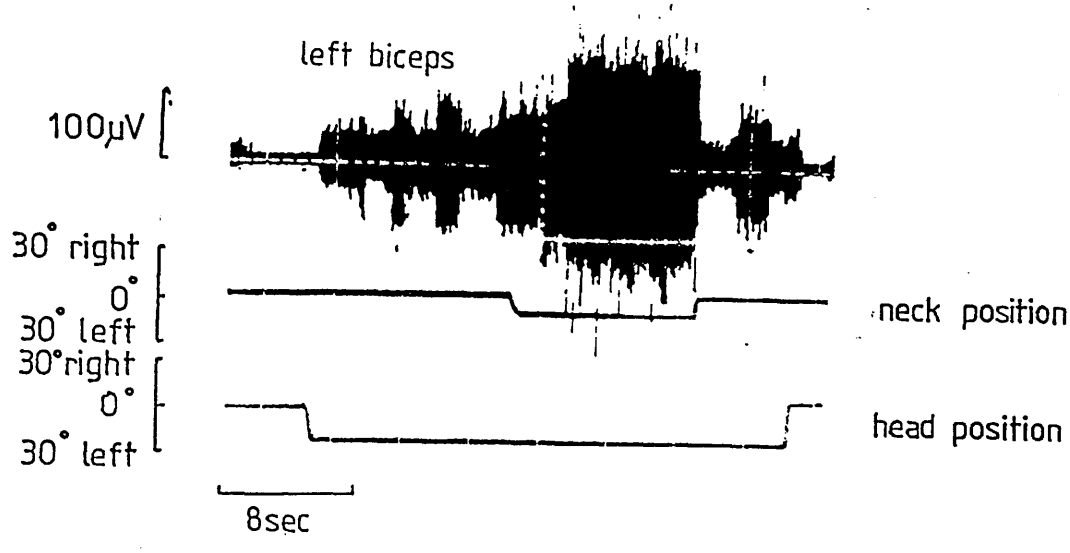


Figure 50. Abnormal and uncommonly observed interaction of labyrinth and neck reflexes in the left biceps (upper trace) resulting from areversal in the labyrinth reflex in this muscle in an acutely hemilabyrinthectomized cat. Neck and head position shown by middle and lower traces respectively: (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut).

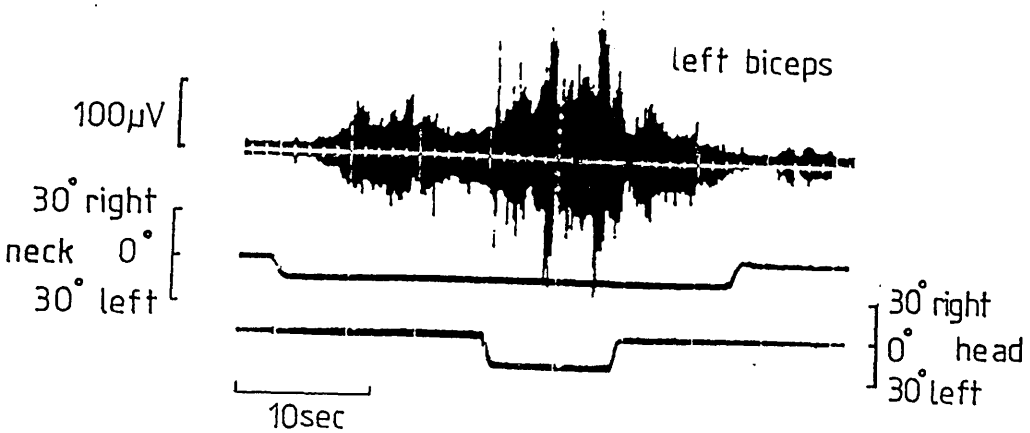


Figure 51. As figure 50 (same animal). Labyrinth and neck reflexes in left biceps of an acutely hemilabyrinthectomized cat: (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut).

pre-existing neck reflex.

This form of labyrinth and neck reflex interaction is similar to the behaviour of the right extensors in all acute preparations. Thus in these three animals there would seem to be symmetry in the behaviour of left and right extensors with that observed in the left flexor. These three muscle groups being co-activated with rotations of the head to the left and simultaneously suppressed with tilts that are directed to the right (the right flexor behaving reciprocally).

Hemilabyrinthectomy, therefore, in these three animals has affected the behaviour of all muscle groups except the left extensors. With respect to the normal pattern of labyrinth reflexes the left flexor, right flexor and right extensor muscles show reversals in their reflex behaviour. Thus in these three animals the interactions with neck reflexes act in the same direction. It would appear therefore that in the animals showing this behaviour left labyrinthectomy has a more profound effect on the organisation of labyrinth reflexes than was observed in the majority of cases. Why this should be so is not clear, though it is suggestive that despite only one labyrinth being operational that several pathways relaying labyrinth information, though acting with different signs, are available and in certain circumstances one may dominate over the other, and this may therefore lead to reversal in the form of a particular component of the overall response to head tilt.

3.3.0 The pattern of labyrinth and neck reflexes in chronically left hemilabyrinthectomized cats.

In this section the pattern of reflex response to changes in head and neck position will be described for cats in which the left labyrinth was destroyed at least eight weeks prior to the experiment.

A total of ten animals were used in this study. Out of this number three did not show any signs of labyrinth or neck reflex activity. The remaining seven provide the basis for the results that will be presented. Before describing the reflex activity of these animals a summary of the behaviour of the total collection of animals during the recovery to labyrinthectomy will be given.

3.3.1 Observations on the behaviour and physical signs accompanying left hemilabyrinthectomy.

On arousal from the sedation, given at the time of the operation, all animals developed ocular and head nystagmus. The ocular nystagmus is very strong at this time and is characterised by a fast component directed horizontally to the right with a slow phase directed to the left (ie. toward the lesion). The form of the head movements seen in this early period following the operation are best described as "nodding movements". The appearance of these movements in some ways resemble the form of head movements seen in drowsy humans. These movements giving the appearance of an inability to support the head adequately.

Such that, it falls forward or to the side, until after a certain excursion a violent jerking movement occurs which tends to restore head position to normal, whereupon the whole cycle repeats itself.

For the first twenty four hours after surgery the animals made little attempt to move, preferring to sleep or lie quietly. When attempting movement any one animal could only manage one or two badly coordinated steps before falling over. In most of the cases where I observed early attempts to walk it appeared that any movement of the head precipitated a fall. Most falls being toward the left side of the animal. Thus it is quite apparent in the period shortlyfollowing hemilabyrinthectomy that these animals are handicapped by not only being unable to stabilize their visual field, but are also rendered incapable of executing coordinated movements.

Within forty eight hours following the removal of the labyrinth the ocular nystagmus has either disappeared or is greatly reduced (disappearing completely in all animals after five days) and the exaggerated movements of the head ceased. The attitude of the head is far from normal, and is held tilted to one side. The tilt is directed towards the lesion and in my experience does not recover with time. An example of this head tilt is shown in Plate 1 (this photograph was taken 36 hours after the operation).

After the nystagmus has ceased animals tend to remain inactive, although less so than during the first day. When cats make an effort to stand their weight is

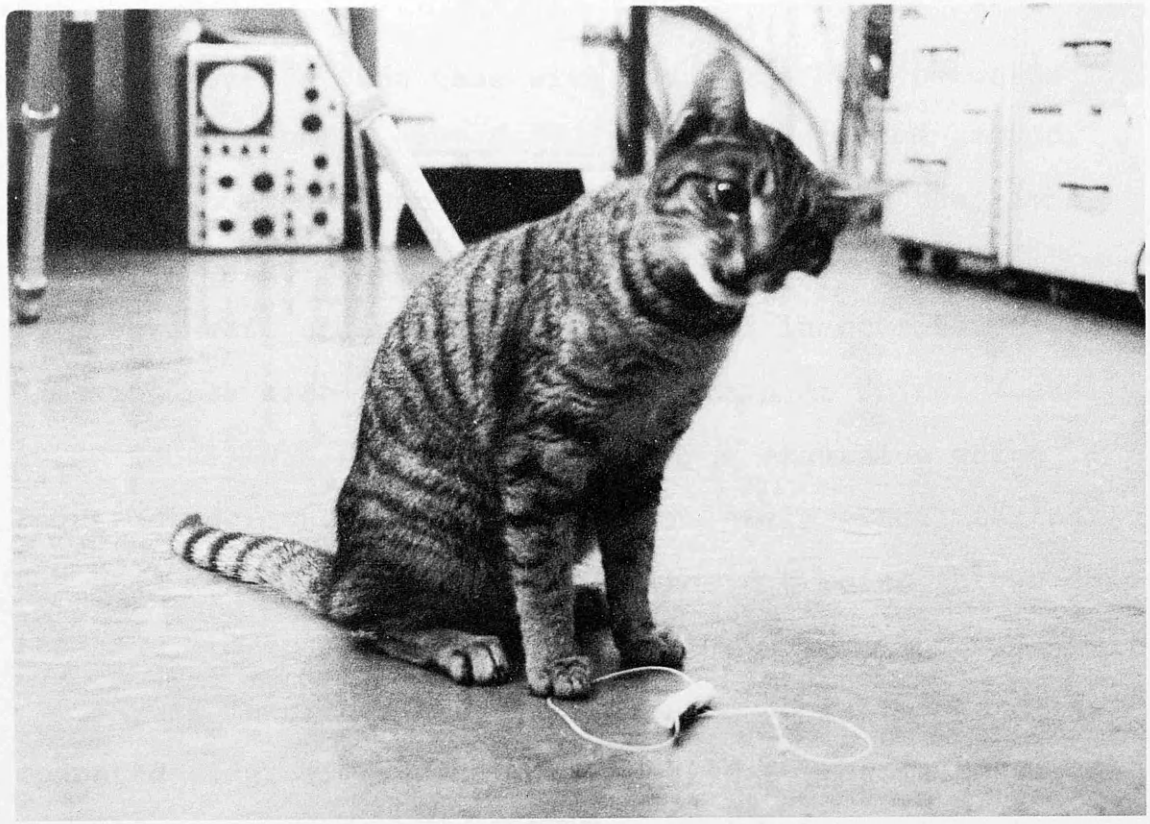


Plate 1. Photograph of acute hemilabyrinthectomized cat illustrating characteristic head tilt (36 hours after labyrinthectomy).

supported over a wide base with the limbs held outwards from the body. Also, the body is held low to the ground, and it is common to observe distinct tremor in the limbs during standing. From such a position any exploratory movements were observed to be jerky and inaccurate. Visual tracking was also impaired, in that when an object (usually a toy mouse) was moved through a large excursion which required movements of the head to maintain visual contact the head movement would result in the cat being thrown onto its side.

As mentioned above cats tended to fall toward the operated side, if pressure was applied to the left side of these animals (as if to push to the right) considerable resistance was met. The extensors of the right side showing considerably more tone than those of the left. In many instances cats would use the side of their cage or a wall as a support to the left side and by doing this were able to move around without falling over.

Within the first post-operative week, each day saw the cats become more lively, and at the end of this period most cats were able to move around quite effectively in both their cages and in the laboratory. Although locomotion was possible, there were still apparent differences from normal. The animals during walking would walk with the limbs slightly splayed from the body and keep low to the ground. The gait was also abnormal in that the whole of the hind foot was used rather than the toes during the support phase. An idea of the differences in gait can be seen by comparing the photographs of the normal and

hemilabyrinthectomized cat in Plates 2 and 3. In the labyrinthectomized cat the head tilt and the wide and low stance are clearly seen.

Postural deficits are also apparent when cats, through their own curiosity, are required to jump from one surface to a lower one. On landing the cats usually fall on their face and then onto their side. Appearances suggesting that forelimb tone before and during landing is not sufficient to prevent the collapse of the animal.

In the weeks following this early period the postural deficits diminish, though if suddenly surprised by a sound from one side a quick head movement can cause a loss of balance. Similarly jumps are also capable of courting disaster. However, given sufficient time it becomes increasingly difficult to distinguish these cats from normal cats, the appearance of these animals following two months of recovery is such that even these long lasting deficits are compensated for in most respects, although it should be restated that head tilt persists.

3.3.2 Reflex reactions to alterations in head and/or neck position in chronic hemilabyrinthectomized preparations.

The previous section has dealt with how, given time, the observable postural deficits following unilateral labyrinthectomy diminish. In this section the reflex reactions to head and neck tilts of various forelimb muscles are decribed in the 'compensated' animal.

In the seven experiments that these results are

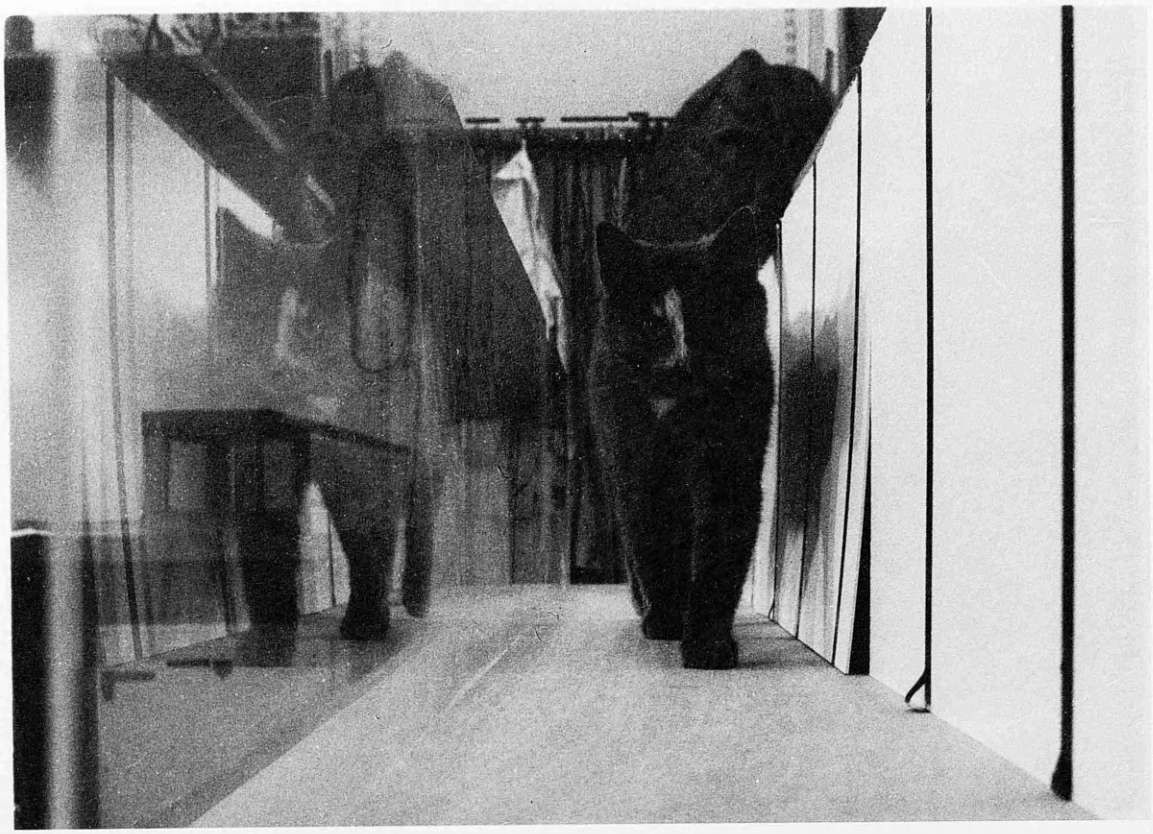


Plate 2. Photograph of a normal cat walking.

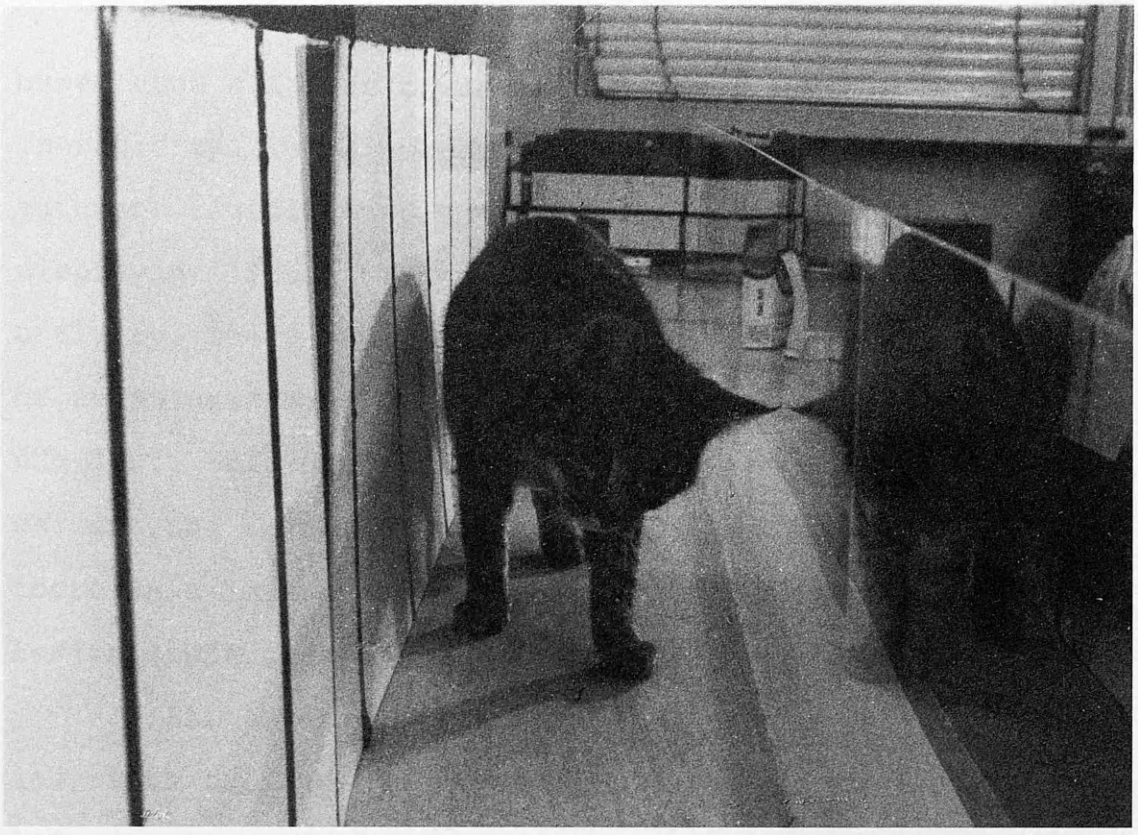


Plate 3. Photograph of hemilabyrinthectomized cat walking (2 days after labyrinthectomy).

based upon all cats on decerebration displayed an asymmetry in rigidity. The limbs on the left side showing intense extensor rigidity and the limbs on the right side displaying little extensor tone but considerable flexor activity. The unrestrained decerebrate assuming the posture of an animal standing, side on, upon a gradient sloping to the left. This distribution of rigidity is opposite to that encountered in acute hemilabyrinthectomized animals where there is a loss of extensor rigidity on the side of the lesion (left side).

All seven cats showed the normal pattern of labyrinth reflexes in the extensor muscles of the right and left forelimbs during the course of an individual experiment. Fig. 52 shows the response of the right medial triceps to a head rotation to the left (C1 and C2 cut, axis vertebra clamped). The EMG trace clearly shows the silencing of a single motor unit during the period of the tilt and its sudsequent reappearance on returning the head toward the starting position. This type of behaviour is identical in form to that of right extensors in cats with two functioning labyrinths and is in the opposite direction to reflexes seen in these muscles in acute preparations. As in normal, and acute animals, the left extensor muscles show increased motor output with head rotations to the left. Fig. 53 shows such an increased discharge in the left triceps following rotation of the head to the left. This tonic response is therefore acting reciprocally to that operating in the right extensor following head rotations.

The labyrinth reflexes acting on forelimb extensors

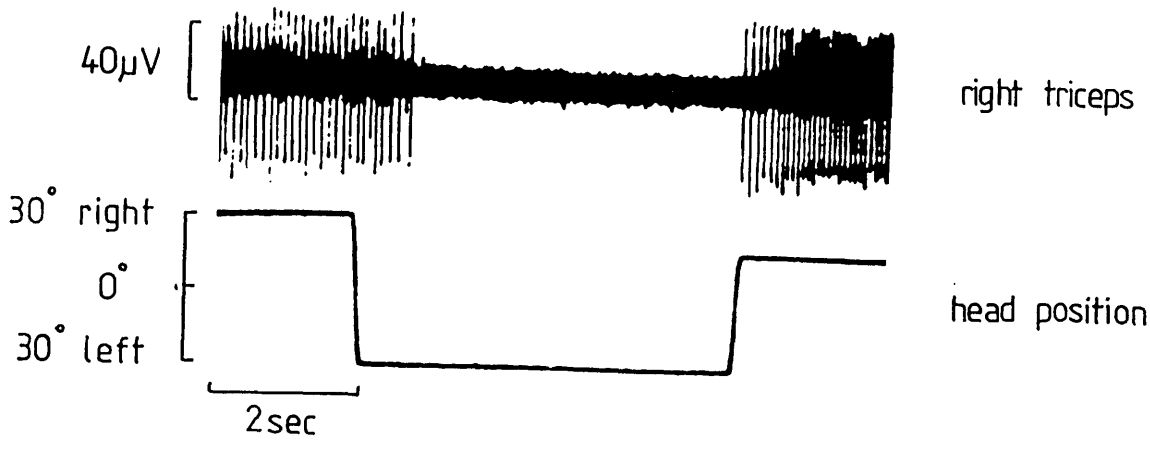


Figure 52. EMG from the right triceps (upper trace) on head rotation in a chronically hemilabyrinthectomized cat: (left hemilabyrinthectomy carried out 8 weeks prior to decerebration, C1 & C2 cut, axis vertebra clamped).

closely parallel those observed in normal cats despite the loss of one labyrinth. Neck rotations also act as normal, in that, rotation of the axis vertebra causes reciprocal activity that acts in an antagonistic direction to labyrinthine reflexes. This is illustrated for the right extensor in Fig. 54 and for the left extensor in Fig. 55. In Fig. 54 a rotation of the neck to the right silences pre-existing EMG activity in the right triceps, but on subsequent head tilt in the same direction this EMG activity is re-established. The response shown in Fig. 55 depicts a similar antagonism between labyrinth and neck reflexes in the left triceps (medial head). The raw EMG and the rectified and integrated EMG are illustrated, the figure shows a distinct labyrinth reflex being abolished by the action of a neck reflex. Rotation of the head to the left is seen to cause an increase in EMG from this muscle, this increase is then subsequently negated following a rotation of the axis vertebra to the left. On subsequently returning the axis to its previous position the labyrinth reflex is again revealed, the reflex maintaining until the head is returned to its original position. The demonstration of this antagonism between labyrinth and neck reflex systems establishes that in these animals the normal pattern of labyrinth reflexes exists and the form of interaction with these reflexes is evidence for the existence of a compensatory mechanism. The compensation operating to allow the remaining labyrinth to influence the extensor musculature in a reciprocal manner that is appropriate for the development of asymmetric reflexes.

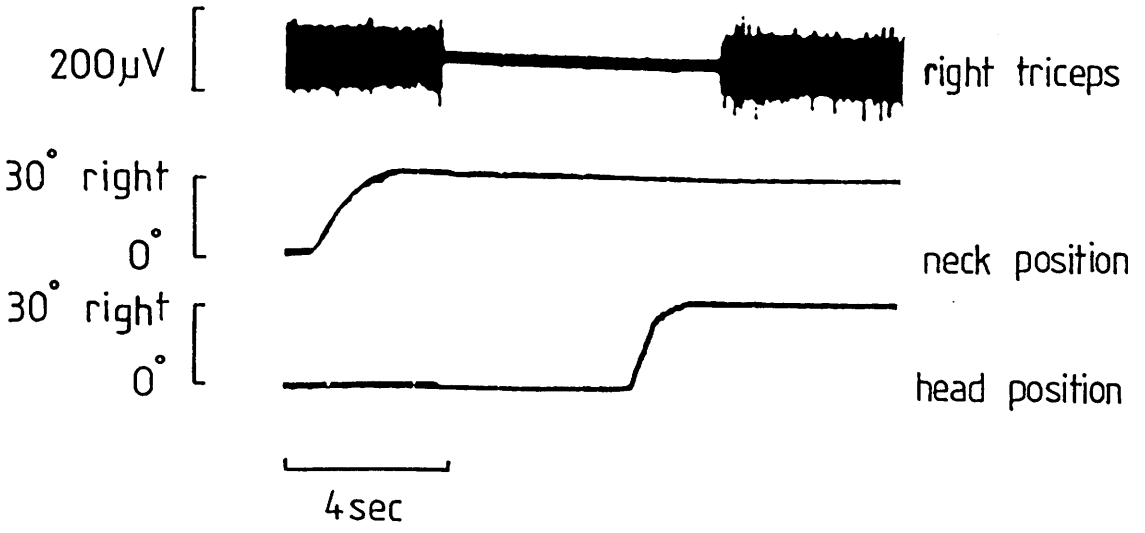


Figure 54. Normal pattern of labyrinth and neck reflexes in the right triceps (upper trace) of a chronically hemilabyrinthectomized cat. Neck and head position are shown by the middle and lower traces respectively: (left hemilabyrinthectomy performed 12 weeks prior to decerebration, C1 & C2 cut).

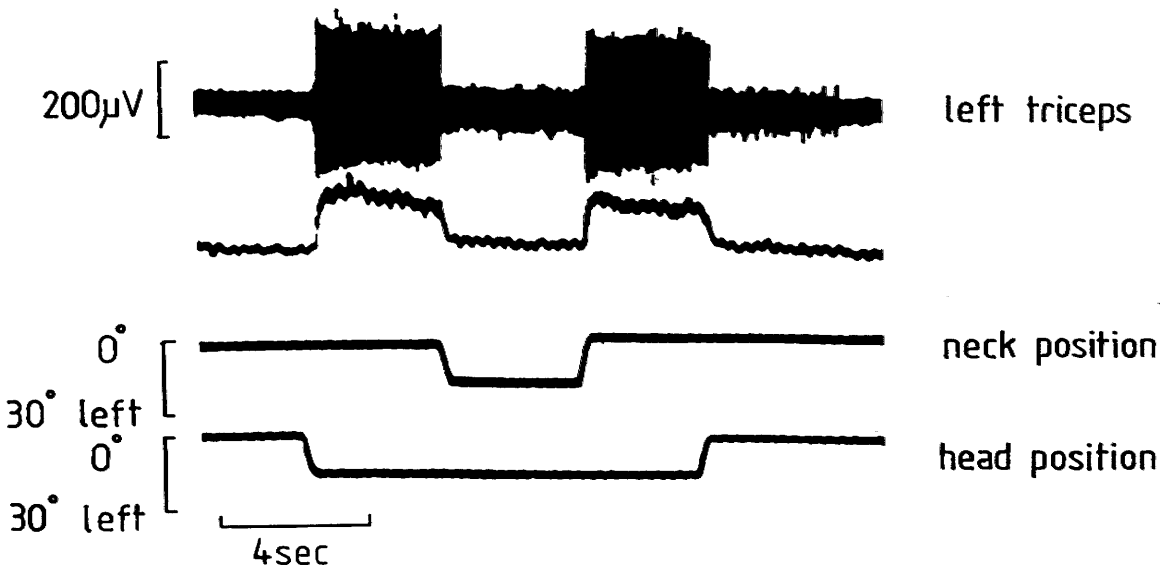


Figure 55. Normal pattern of interaction between labyrinth and neck reflexes in the left triceps (raw EMG is illustrated along with the rectified and integrated EMG in the upper two traces). Neck and head position are shown by the lower traces: (left hemilabyrinthectomy performed 32 weeks prior to decerebration, C1 & C2 cut).

The relationship between the activity induced in the left extensor and in the right flexor is also as found in preparations with intact labyrinths. Fig. 56 shows the EMG recorded from the left triceps (top trace) and right biceps during successive tilts of the head to the left. The figure illustrates that these muscles are synchronously active on head tilts left side-down. The right limb becoming flexed during rotations of the head to the left. With rotations to the right the activity in the right flexor diminishes. Thus the right flexor behaves with the normal form of response to head tilts.

Fig. 57 shows the pattern of reflexes in the right brachialis. With rotation of the head to the right there is a suppression of EMG activity while a tonic increase in activity accompanies tilts directed towards the left. This form of labyrinth reflex represents a reversal in the direction of response from that observed in the acute animal. With this return to the normal pattern of labyrinth reflex the reflex interaction between neck and labyrinth reflexes, as illustrated in Fig. 58, appear normal. The figure depicts a large increase in EMG on head rotation to the left. This increse is however interrupted by neck rotation to the left, which acts to suppress the existing labyrinth reflex. The antagonism betweeen neck and labyrinth reflexes acting on the right flexors is easily observed in this figure (58) and highlights, how, through time the labyrinth reflex is re-established to provide a normal form of reflex interaction in right flexors.

The behaviour of the left extensor and of the right

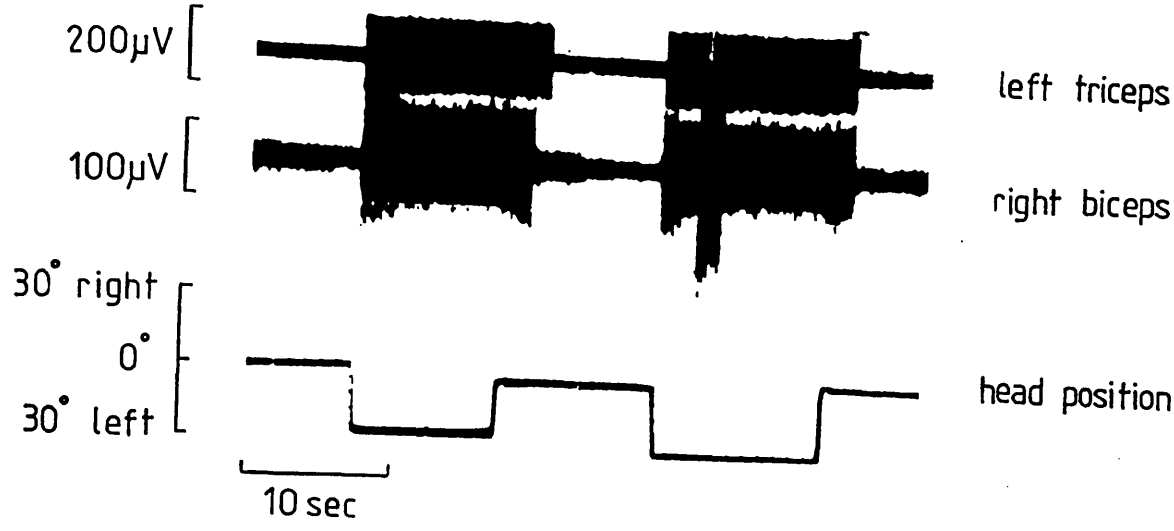


Figure 56. Co-activation of left triceps (top trace) and right biceps (middle trace) on rotation of the head in a chronically hemilabyrinthectomized cat: (left hemilabyrinthectomy performed 8 weeks prior to decerebration, C1 & C2 cut, axis vertebra clamped).

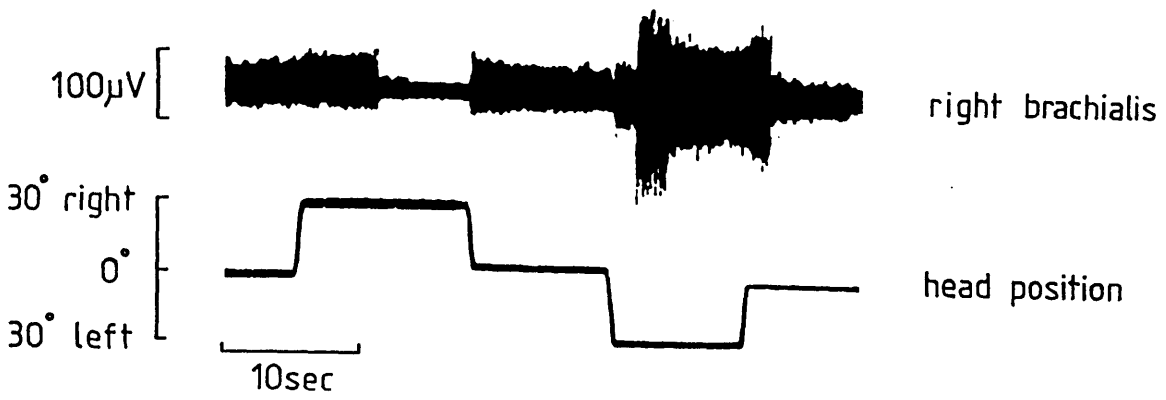


Figure 57. Normal pattern of labyrinth reflex in the right brachialis (top trace) on rotation of the head (bottom trace) in a chronic hemilabyrinthectomized cat: (left hemilabyrinthectomy performed 14 weeks prior to decerebration, C1 & C2 cut, axis vertebra clamped).

Figure 58. Normal form of interaction between labyrinth and neck reflexes in the right biceps (upper trace) of a chronically hemilabyrinthectomized cat on rotation of the neck (middle trace) and of the head (lower trace): (left hemilabyrinthectomy performed 14 weeks prior to decerebration, C1 & C2 cut).

extensor and flexors can be seen from the above results to closely correspond with the direction of responses obtained in normal cats following head or neck rotation. Intuitively, one might therefore expect that the left flexor would also conform to this scheme and act, in terms of motor output, in a manner equivalent to what is observed in cats with intact labyrinths. The actual responses observed in the left flexors are outlined below.

Of the seven animals in which signs of positional reflexes could be observed, three did not show any sign of labyrinth or neck reflex activity in flexor muscles of the left forelimb. In these animals the degree of extensor rigidity was very high on the left side, and it is probable that no reflexes were seen in these muscles due to high levels of reciprocal inhibition. The lack of any spontaneous EMG in the flexors of these cats would seem to support this view. However in four cats activity could be recorded in the left flexors, but unexpectedly the activity changes seen during head tilts were reversed from the normal pattern. Fig. 59 shows an example of the activity changes observed in left biceps following rotations of the head. From this figure it is seen that rotation to the left increases EMG output, while rotation to the right has the opposite effect. This behaviour is opposite to that of a normal cat, and to that seen in the majority of acute hemilabyrinthectomized cats. Consequently it would be expected that head rotations would influence right and left flexors in chronic animals in the same sense. Similarly, it would also be expected that the left extensor would become

Figure 59. Reversed pattern of labyrinth reflex in the left biceps (upper trace) of a chronically hemilabyrinthectomized cat on rotation of the head (lower trace): (left hemilabyrinthectomy performed 32 weeks prior to decerebration, C1 & C2 cut, axis vertebra clamped).

active together with the left flexor during side-down tilts. A reversed labyrinth reflex in the left flexors also, as can be seen in other muscles in acute animals, has strong implications for the pattern of reflex interaction with neck reflexes acting on this muscle. In the following figures the reflex output of the left flexors during head and neck rotations will be compared with responses recorded simultaneously from other muscles.

Fig. 59 illustrated that rotations of the head to the left caused increased EMG from the left flexor, in Fig. 60 similar behaviour is shown in the rectified and integrated EMG record. In this figure the response recorded from the right biceps is also shown. The figure illustrates the interaction of labyrinth and neck reflexes in these two muscles. As seen in previous Figs. (55, 56 & 57) the right flexor shows an increased output with head tilt to the left and a subsequent reduction in output when a neck rotation to the left is added. The behaviour of the left biceps on head rotation is reversed from normal with the integrated EMG showing an increase in activity on rotating the head to the left. With the addition of a neck rotation there is a reduction in motor activity such that the response in the left flexor (Fig. 60, lower EMG trace) resembles that seen in the right flexor (Fig. 60, upper EMG trace). This form of interaction in the left flexor between labyrinth and neck reflexes is indicative that in addition to a reversal in the direction of the labyrinth reflex, a reversal in the neck reflex acting on this muscle has also occurred in the compensatory process. In acute preparations examples of

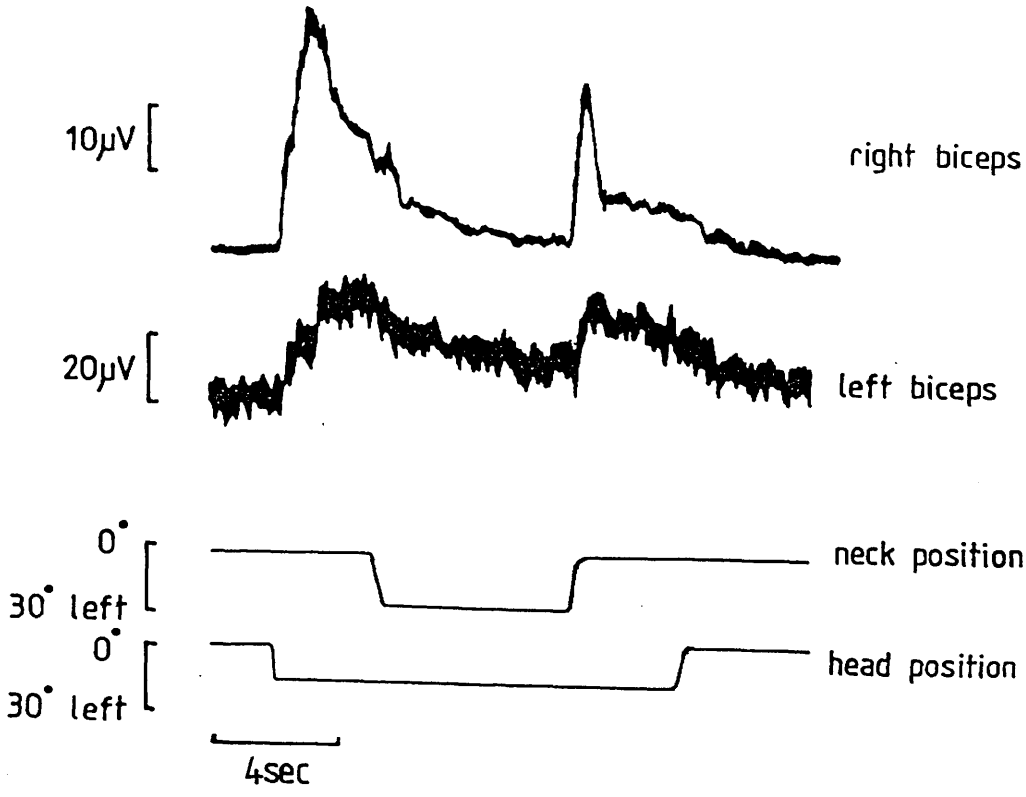


Figure 60. Interaction of labyrinth and neck reflexes in the right and left biceps in a compensated hemilabyrinthectomized cat. Note that in the left biceps the labyrinth and neck reflex is reversed in comparison to the normal pattern. Rectified and integrated EMG recorded from right and left biceps on independant rotations of the head and axis vertebra: (left hemilabyrinthectomy performed 14 weeks prior to decerebration, C1 & C2 cut).

reversed labyrinth reflexes in the left flexors were occasionally observed however, in all these examples the addition of a neck tilt to the left resulted in further increases in EMG activity (see Figs. 50 and 51). While in this example both labyrinth and neck reflexes have reversed and so preserved the 'normal' antagonism between these reflex systems. Consequently a head rotation results in symmetrical changes in activity between flexors and extensors of the left limb, with neck reflexes also acting synergistically (though antagonistic to labyrinth reflexes) on these muscles. Thus head tilts may act to modulate the stiffness of the left limb through co-activation of extensor and flexors rather than altering the distribution of tone through a reciprocal relationship. In addition since the neck reflex also appears to act on these muscles postural stability can still be maintained though acting through a different strategy than in normal cats.

In further support for this scheme of interactions between flexor and extensor in the left limb it was noticed in three of the chronic animals that a head tilt could induce locomotor like activity in forelimb muscles. Records from such activity show that when recording from opposite limbs, bursts of EMG could be seen. These phasic EMG cycles were induced by tilting the head to the right and could be terminated by returning the head to the starting position. Fig. 61 illustrates such activity within the right (top EMG trace) and left (lower EMG trace) triceps. From this figure the bursts of activity can be seen to be out of phase in the different limbs. This in an unrestrained animal

Figure 61. Phasic EMG bursts induced in forelimb extensors by rotation of the head. EMG recorded from right (upper EMG trace) and left (lower EMG trace) triceps on rotation of the head to the left (lower trace) in a chronically left hemilabyrinthectomised cat. Note that EMG bursts occur out-of-phase in the different muscles: (left hemilabyrinthectomy performed 18 weeks prior to decerebration, C1 & C2 cut, axis vertebra clamped).

resulting in alternating extension of right and left forelimbs. Furthermore it would appear that in the left limb the bursts of activity arise from the recruitment of previously silent motor units, while in the right limb the appearance of the EMG is suggestive of motor units which were active prior to the head tilt becoming periodically silenced. In this way a parallel between tonic labyrinth reflexes can be seen, the head rotation thus may be acting asymmetrically on the opposite extensors. Bearing this in mind, when the EMG is recorded simultaneously from left triceps and left biceps during this type of behaviour, one finds that rather than a reciprocal relationship of extension followed by flexion there is co-activation of these normally antagonistic muscles. An example of this is illustrated in Fig. 62. In this figure a head tilt to the left is again seen to induce phasic bursts of EMG activity. These bursts of EMG ceasing when the head is returned to the normal position. The EMG from the left triceps is shown by the top trace while that from the left biceps is shown immediately below. Clearly the EMG bursts are phase locked to one another indicating a synchronisation of activity in flexor and extensor during the head tilt to the left. Interestingly these phasic bursts of activity are suppressed by neck rotation to the left. This is illustrated in Fig. 63. Following head rotation to the left the EMG from the left triceps and biceps (upper and lower EMG traces respectively) again show synchronised bursts of activity, these episodes of activity are however completely suppressed following a rotation of the neck to the left,

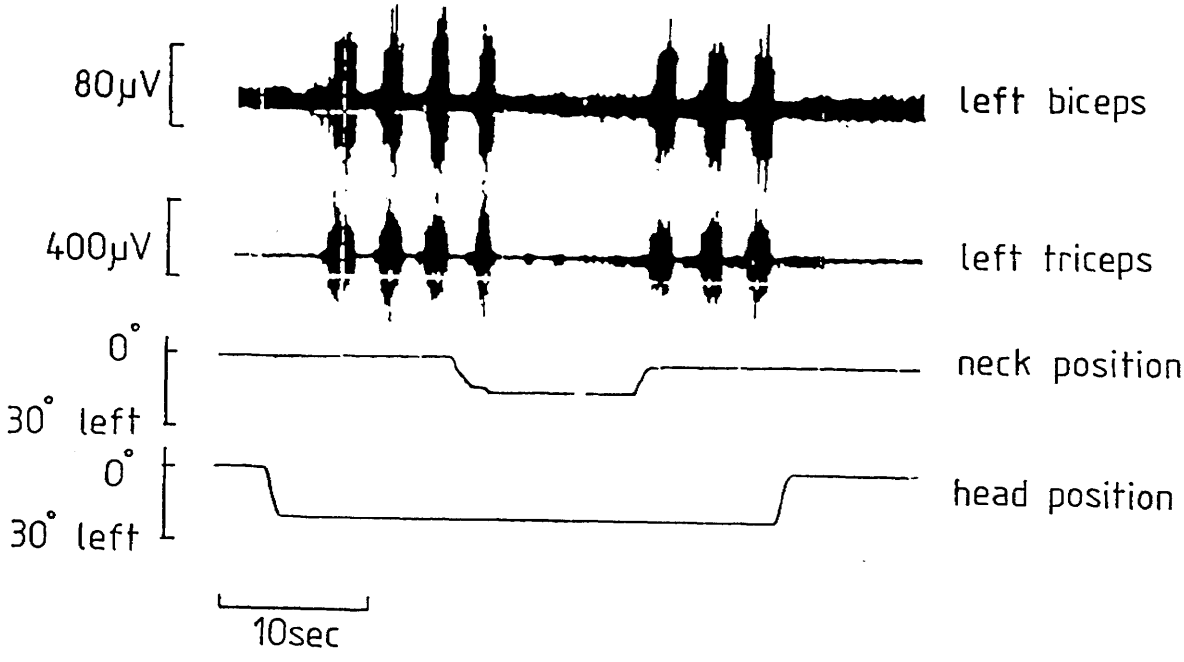


Figure 63. Synchronous phasic bursts of EMG activity in left triceps and biceps induced by head rotation and suppressed by neck rotation. EMG recorded from left biceps (upper EMG trace) and left biceps (lower EMG trace) on rotation of the head, then neck to the left (neck and head position are indicated by the lower two traces respectively): (left hemilabyrinthectomy performed 18 weeks prior to decerebration, C1 & C2 cut).

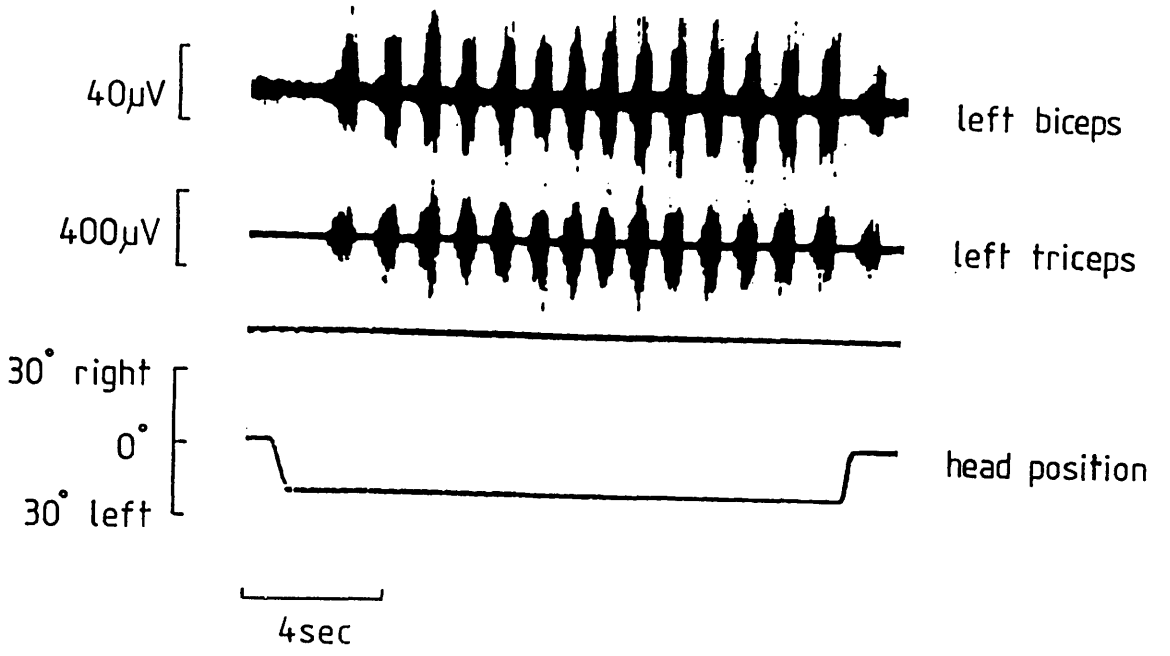


Figure 62. Synchronous phasic bursts of EMG activity in left triceps and biceps induced by rotation of the head. EMG recorded from left biceps (upper trace) and left triceps (middle trace) on rotation of head to the left (lower trace) in a chronically hemilabyrinthectomized cat: (left hemilabyrinthectomy performed 18 weeks prior to decerebration, C1 & C2 cut, axis vertebra clamped).

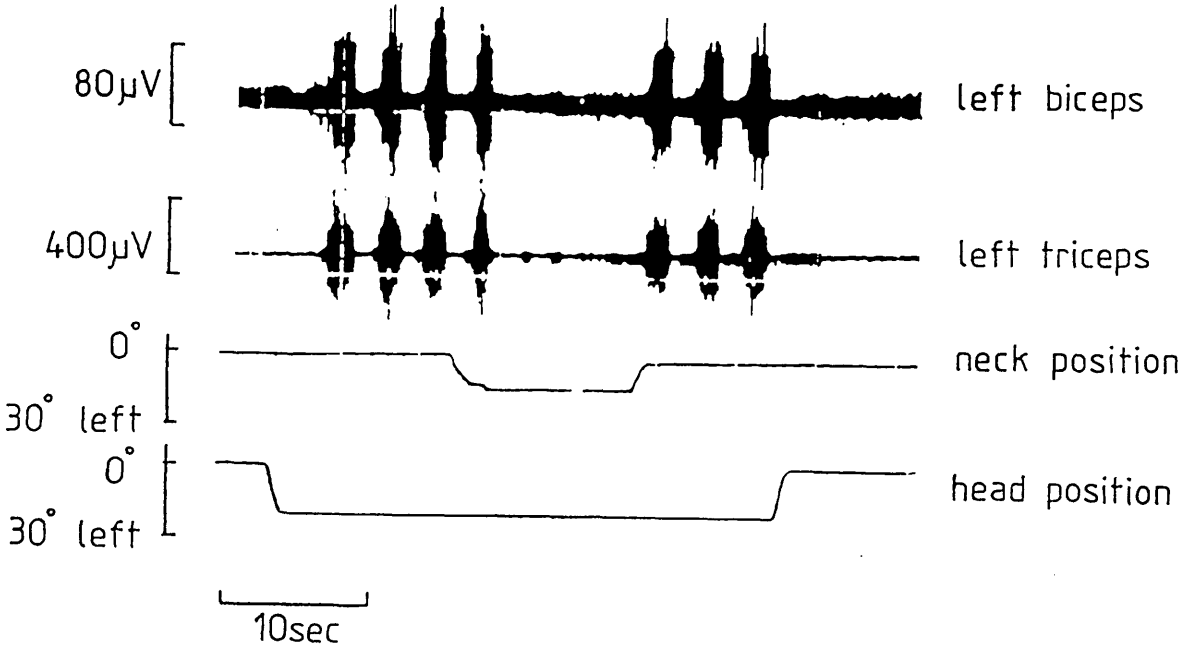


Figure 63. Synchronous phasic bursts of EMG activity in left triceps and biceps induced by head rotation and suppressed by neck rotation. EMG recorded from left biceps (upper EMG trace) and left biceps (lower EMG trace) on rotation of the head, then neck to the left (neck and head position are indicated by the lower two traces respectively): (left hemilabyrinthectomy performed 18 weeks prior to decerebration, C1 & C2 cut).

although they subsequently reappear on moving the neck back to the mid-position. These phasic bursts of EMG only ceasing when the head is returned to the normal position. Although these figures do not illustrate tonic labyrinth or neck reflexes, as such, they do show that in the chronic cat labyrinth and neck influences can affect the left and right extensors in a manner similar to the action of the tonic reflexes, and therefore these figures provide further demonstration that the labyrinth and neck influences are reversed in the left flexor in chronic left hemilabyrinthectomized cats. In addition these figures also show that changing head or neck position can influence pattern generators and may indicate a common interneuronal pathway between the tonic reflexes and the neuronal circuitry that generates locomotor patterns.

In summary it would appear that in the chronic cat a compensation to the left labyrinthectomy has occurred. This compensation restores the abnormal form of labyrinth reflexes observed in the right forelimb of acute preparations to the normal pattern seen in cats with intact labyrinths. While in the left forelimb there is a reorganisation of the reflex actions from the labyrinth and neck during the compensation period. The left extensor retaining normal behaviour but the left flexor displaying a reversed labyrinth and neck reflex. The pattern of labyrinth and neck reflexes in the chronic cat are shown in table V. This scheme of reflexes although varying from that observed in cats with intact labyrinths can still be considered as a system through which postural stability can

	Chronic hemilabyrinthectomy			
	Right limb		Left limb	
	Extensor	Flexor	Extensor	Flexor
Head rotation to right	↑	↓	↓	↓
Head rotation to left	↓	↑	↑	↑
Neck rotation to right	↓	↑	↑	↑
Neck rotation to left	↑	↓	↓	↓

Table V. Summary of effects produced by rotations of the head or neck on the EMG activity of elbow extensors and flexors in chronic left hemilabyrinthectomized cats. The arrows indicate increased or decreased activity.

be maintained (see discussion).

3.4.0 Observations on eye movements resulting from hemilabyrinthectomy.

It is well documented that a nystagmus of the eyes develops following unilateral labyrinthectomy. In this section of the thesis some observations are presented describing these eye movements in acute and chronic hemilabyrinthectomized cats. All recordings of nystagmus were made following decerebration.

Observations on the group of animals selected for the study on compensation to unilateral labyrinthectomy revealed that in every case a nystagmus developed on recovery from the anaesthesia. On watching these eye movements it was clear that the slow component was directed towards the side of the lesion (i.e., toward the left). Just as the nystagmus could be observed in conscious cats during acute stages of recovery, nystagmus could be recorded in decerebrate animals immediately following hemilabyrinthectomy. Fig. 64 gives an example of the form of the nystagmus in these preparations and like observations made on 'intact animals' the nystagmus again is characteristically seen to show a slow drift toward the right. The frequency and the amplitude of these rhythmic eye movements is shown in this figure to be dependant on the position of the head. Tilts to the right increase the beat frequency, and greatly reducing the amplitude, although rotations to the left do not greatly influence the

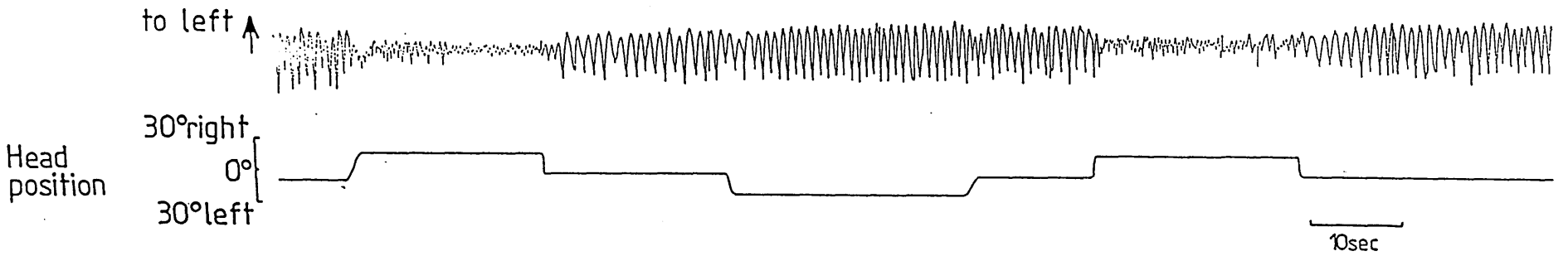


Figure 64. Nystagmus recorded in an acute left hemilabyrinthectomized cat showing slow component directed to the left and modulation of nystagmic frequency and amplitude with rotation of the head: (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

frequency or amplitude of the nystagmus to a significant degree. The effect of head position on the frequency of nystagmus is shown in Fig. 65 which illustrates a histogram depicting the number of nystagmic beats made in consecutive two second bins. The rotations to the right more than doubling the basic beat frequency. No clear effect is seen with rotations to the left but this may be simply due to the level of variability in the nystagmus with the head in the normal position.

The nystagmus seen following hemilabyrinthectomy in the acute stages in the behaving cat disappears several days after the lesion. Recognised as the earliest sign of compensation to the lesion this nystagmus does not reappear if no other surgical intervention is made. However, decerebration at any time after the initial operation releases a nystagmus much like that observed in the acute stage. In Fig. 66a an example of this nystagmus is illustrated. The decerebration in this example was carried out eight months after the initial hemilabyrinthectomy. The nystagmus resulting in these animals again shows a slow component that is directed towards the left, and shows some dependance on the position of the head. Although not so easily seen as that in the acute example there are small increases in frequency with tilts to the right and decreases with tilts to the left. Although not systematically studied, it is not surprising that changes in head position alter nystagmus, since the drive to the centres responsible for the nystagmus will alter with head position. The important result here is not that frequency

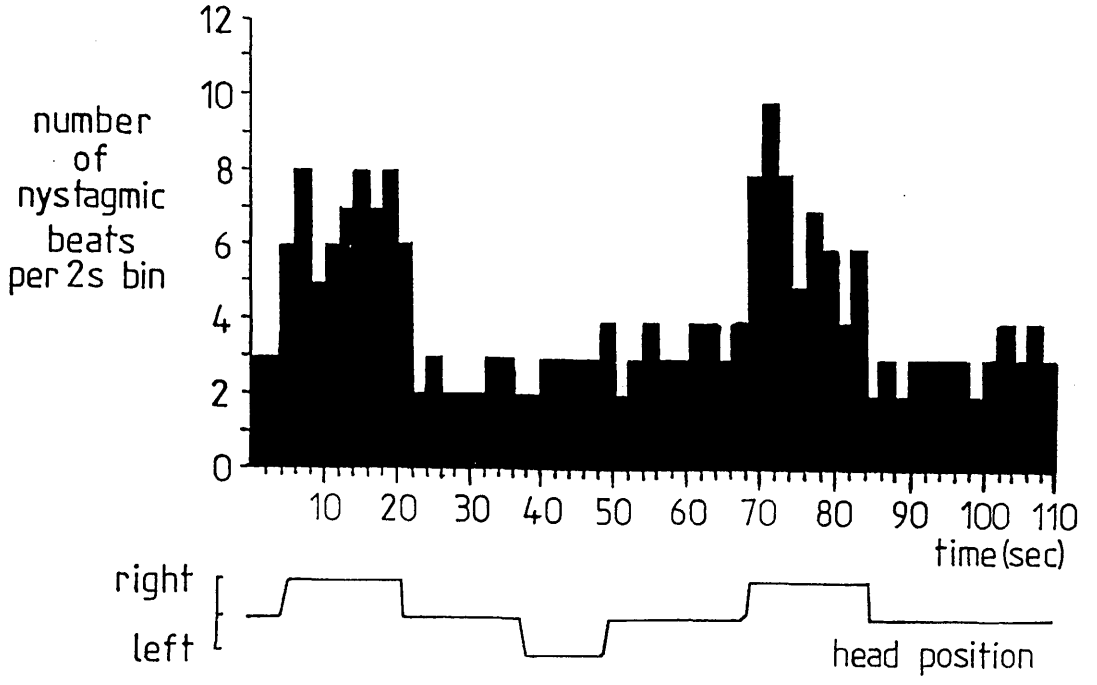


Figure 65. Graph illustrating alterations in the frequency of nystagmus with changes in the position of the head in an acute left hemilabyrinthectomized cat. Frequency is plotted as the number of nystagmic beats occuring within two second intervals. The data on which this graph is plotted is illustrated in Fig 64: (left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut).

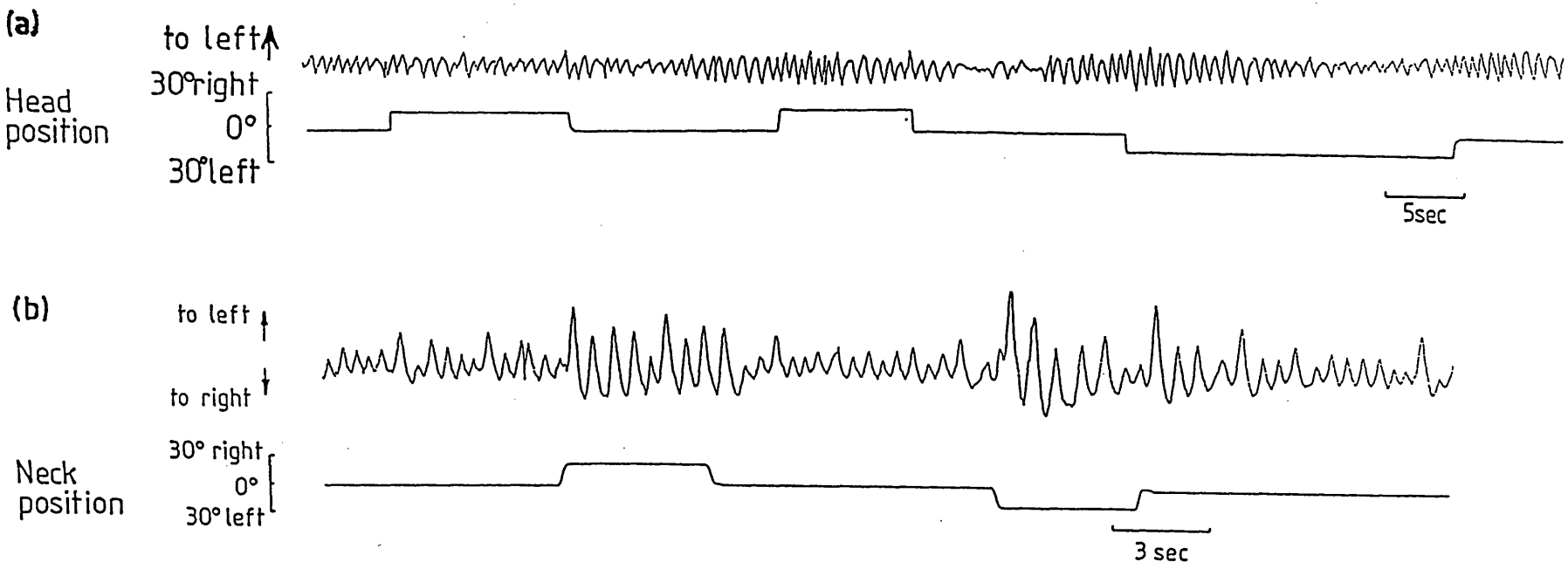


Figure 66. (a) Nystagmus recorded in a chronic left hemilabyrinthectomized cat following decerebration. The slow component is directed toward the left side (ie. the side of the initial hemilabyrinthectomy). Some modulation of the nystagmus is apparent with rotation of the head (head position is shown in the lower trace). (b) Nystagmus recorded in a chronic left hemliabyrinthectomized cat on destruction of the remaining labyrinth (right side). In this instance the slow component is now directed toward the right side, and the nystagmus shows modulation with neck position (indicated by the lower trace in Fig 66b): (left hemilabyrinthectomy carried out 32 weeks prior to decerebration and right labyrinthectomy performed 3 hours after the decerebration, C1 & C2 cut).

is altered by changes in head position but that in a compensated animal decerebration releases a nystagmus that is equivalent to that in the acute animals. This is important in that the chronic animals, both intact (from behavioural observations) and from experimental studies following decerebration show compensated postural reflexes. It would therefore appear that the centres responsible for re-establishing ocular and postural stability are different. Ocular stability is therefore dependant in some way on structures rostral to the level of decerebration, while the postural compensation is organised within centres in the brainstem and possibly to some extent the spinal cord.

A second labyrinthectomy, provided a period of compensation has occurred, also results in the generation of a nystagmus. With this nystagmus known as 'von Bechterews compensatory nystagmus' the slow component is directed toward the side of the second labyrinthectomy. An example of this form of nystagmus is illustrated in Fig. 66b. In this figure a second labyrinthectomy was carried out several hours after decerebration. Prior to the destruction of the remaining labyrinth the nystagmus was directed to the left (as in fig 66a) but immediately after the remaining labyrinth was destroyed the slow component was directed to the right. In the example illustrated activation of neck proprioceptors were seen to alter the nystagmus. It appears that neck rotation (irrespective of direction) results in small frequency reductions and increases in amplitude of nystagmic beats. This

demonstrating the existence of some neck afferent convergence onto centres responsible for the generation of nystagmus.

In summary it can be stated that nystagmus can be seen in the acute stages following unilateral labyrinthectomy and is again evident in the compensated animal following decerebration. The slow component, in each case, is directed toward the side of the lesion though in the compensated animal if a second labyrinthectomy is performed the direction is reversed and the slow phase is directed toward the new lesion. In each example, the nature of nystagmus can be altered by changing the drive from afferent systems projecting to the centres responsible for the generation of the nystagmus. The reappearance of the nystagmus following decerebration and the compensated nature of postural reflexes indicating separate, though not nescessarily totally distinct and independent mechanisms of compensation.

3.5.0 The modulation of labyrinth and neck reflex systems by changes in limb position.

In this section results will be presented which describe how by conditioning crossed extensor and flexion withdrawal reflexes with changes in head or neck position the pattern of labyrinth and neck reflexes can be revealed in forelimb muscles when no direct motor response to positional changes of the head or neck can be observed. In addition, comparisons between protective reflexes evoked at

combinations of head, neck and elbow position will be made in order to assess the influence limb position may have on the tonic conditioning influence from the labyrinth and neck. Results will be presented from experiments carried out on normal and acute preparations.

3.5.1 Labyrinth and neck influence on segmental reflexes.

In a previous section (3.1.7) alterations in decerebrate rigidity were described and the effects of changes in the level of rigidity compared to the ease at which labyrinth and neck reflexes could be evoked in forelimb extensors and flexors. Even when no direct response to head tilt could be recorded in the muscle a description of the pattern of labyrinth reflexes was achieved by monitoring crossed extensor reflexes and flexion reflexes at different head positions. Fig. 25 illustrates that when a fixed stimulus is presented to the cutaneous branch of the right radial nerve (at a stimulus judged to be 2-3 times threshold for the fastest conducting afferents in the nerve) the resulting ipsilateral flexion reflex in right biceps and the synchronously recorded crossed extensor reflex in left triceps show modulation in intensity with changes in head position. These intensity changes are entirely consistent with the form of labyrinth reflexes observed in EMG recordings from these muscles. Such an influence on extension and flexion reflexes is also illustrated in Fig. 67. In this figure the left radial nerve is presented with a stimulus train and the reflex

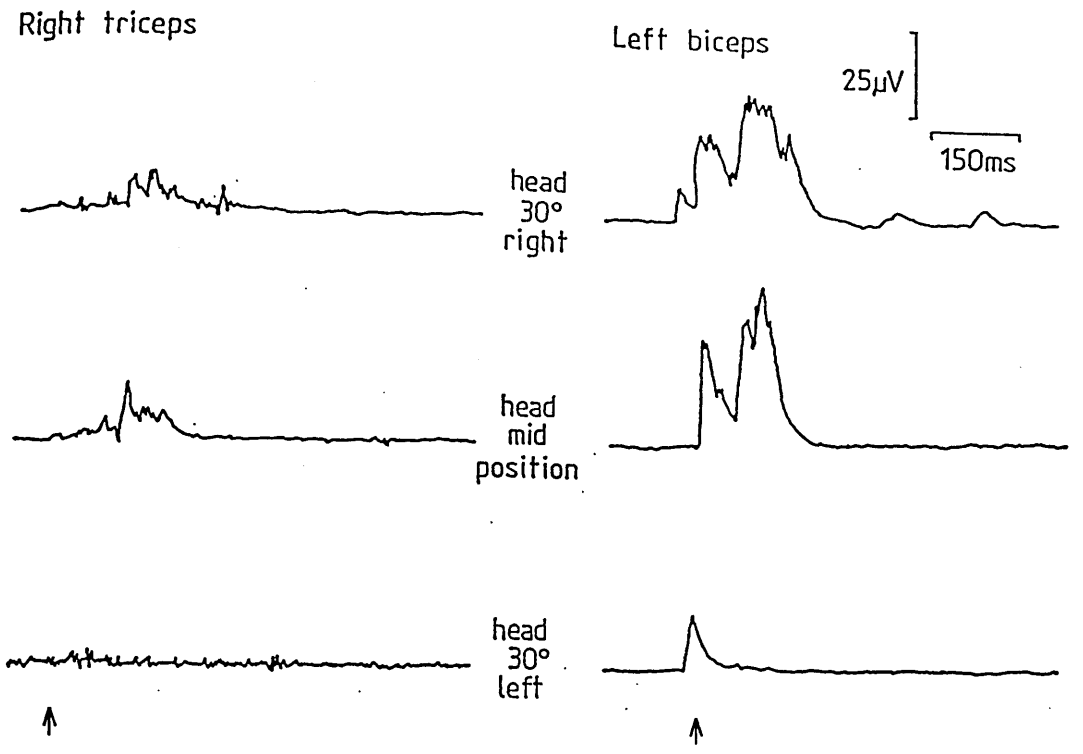


Figure 67. The effect of altering head position on the intensity of simultaneously recorded crossed extensor reflexes and ipsilateral flexion reflexes in the right triceps and left biceps respectively, (illustrated as the rectified and integratd EMG) on electrical stimulation of the dorsal cutaneous branch of the left radial nerve. The stimulus intensity remained fixed throughout the series of recordings. Arrows denote the end of the train of stimulus pulses: (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

response recorded in the right triceps and left biceps at three different head positions. As in Fig. 25 the rectified and integrated EMG records obtained at head positions of 30 degrees right, 0 degrees and 30 degrees left show the characteristic asymmetric pattern of labyrinth reflexes recorded in these muscles. A head tilt to the left suppressing the reflex response in the right extensor and left flexor in Fig. 67, while a similar head position in Fig. 25 results in a facilitation of the reflex response recorded in muscles which are antagonistic to those recorded from in Fig. 67.

Figs. 25 and 67 were recorded from different animals, however, by switching stimuli between right and left radial nerves in the same preparation, and by using comparable amplitudes of stimulation, the labyrinth reflex in one group of forelimb muscles can be studied in each limb and the relationship between the equivalent muscles of opposite limbs assessed. Fig. 68 illustrates labyrinth mediated modulation of flexion reflexes recorded from the right and left biceps following the presentation of comparable stimuli to the dorsal cutaneous branch of right and left radial nerves respectively. Head position, as can be seen from the figure, influences the magnitude of the flexion reflexes in opposite limbs in a reciprocal fashion. The reflex being greatest in one limb when the head is held so that the chin points toward the limb in question (i.e., side-up tilts) while opposite directions of tilt (side-down) produce a reduction in the magnitude of the reflexes. This form of modulation is consistent with direct

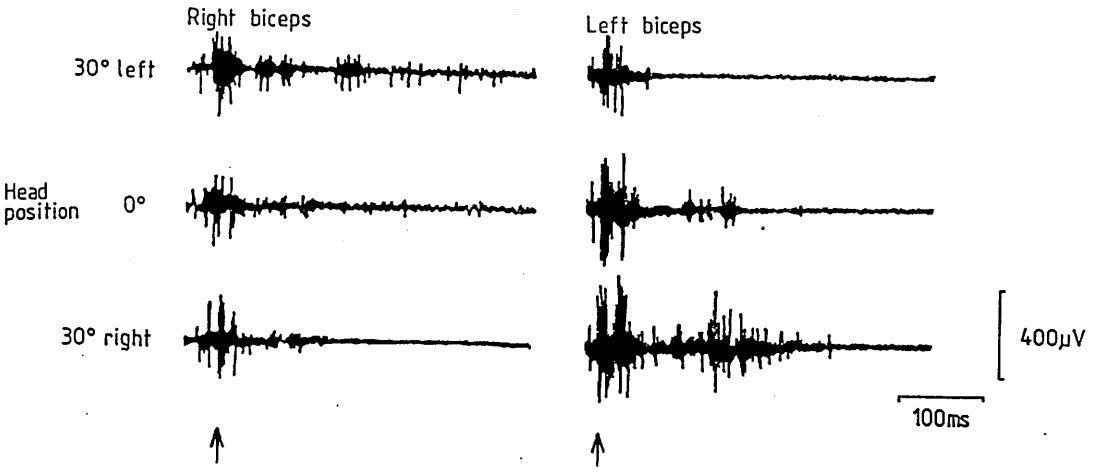


Figure 68. The effect of altering head position on the intensity of flexion reflexes in the right and left biceps (flexion reflexes were provoked by electrical stimulation of the dorsal cutaneous branch of the right and left radial nerves respectively). The stimulus parameters remained constant throughout the series of recordings from right and left biceps. Arrows denote the end of the train of stimulus pulses: (decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

reflex actions resulting from head tilt recorded in these muscles. Thus Figs. 25, 67 and 68 together illustrate that it is possible to determine, by conditioning crossed extensor and ipsilateral flexion reflexes with changes in head position, the nature of the labyrinth influence onto forelimb muscles. In addition, a comparison between these three figures shows that results pertaining to individual muscles from the same and different animals are in agreement, this showing that each muscle has a specific response to different directions of rotation. The conditioning influence of the labyrinth on flexion withdrawal reflexes reflecting the behaviour of labyrinthine induced motor activity in forelimb muscles. Neck reflexes (as are illustrated in later figures) can also be studied in this way.

Alterations in limb position are known to influence the excitability of flexor and extensor reflexes (Baxendale and Ferrell, 1983) therefore by changing limb position it was possible to study the interactions between the descending influence from the labyrinth and neck with those arising from proprioceptors responding to the change in limb position.

3.5.2 Reflex excitability modulation with changes in elbow position.

Prior to presenting results which describe the reflex interactions between labyrinth, neck and elbow position the action of alterting elbow position alone on

crossed extensor and flexion withdrawal reflexes will be considered.

By stimulating the left radial nerve with a fixed stimuli, crossed extensor reflexes can be recorded by EMG in the right triceps brachii. Fig. 69 illustrates how by altering the position of the elbow the reflex response is changed. In Fig. 69a the reflexes are recorded, in order, at elbow positions of 60, 90, 120 and 150 degrees while in Fig. 69b the order of recording is the reverse of this. The figure demonstrates that the reflex response to a fixed stimuli is reduced as the limb is moved from flexed to more extended positions (as in Fig. 69a) and that as the limb is returned to flexed positions (Fig. 69b) there is a facilitation of the reflex at each successively more flexed elbow position. The general conclusion is that flexion tends to facilitate the reflex response recorded in extensor muscles while extended limb positions depress this response. The behaviour of flexion reflexes obtained under similar conditions is opposite to this pattern. Fig. 70 illustrates three flexion reflexes recorded from the left biceps following electrical stimulation of the left radial nerve. The reflexes in this example were recorded with the left elbow joint held at 60, 90 and 150 degrees. It can be seen that the reflex becomes progressively larger as more extended positions are taken up. The directions of modulation of reflex intensity illustrated in Figs. 69 and 70 (observed using a fixed strength of stimulus) show that a reciprocal influence from limb position acts on flexion and extensor reflex pathways. This modulation of these

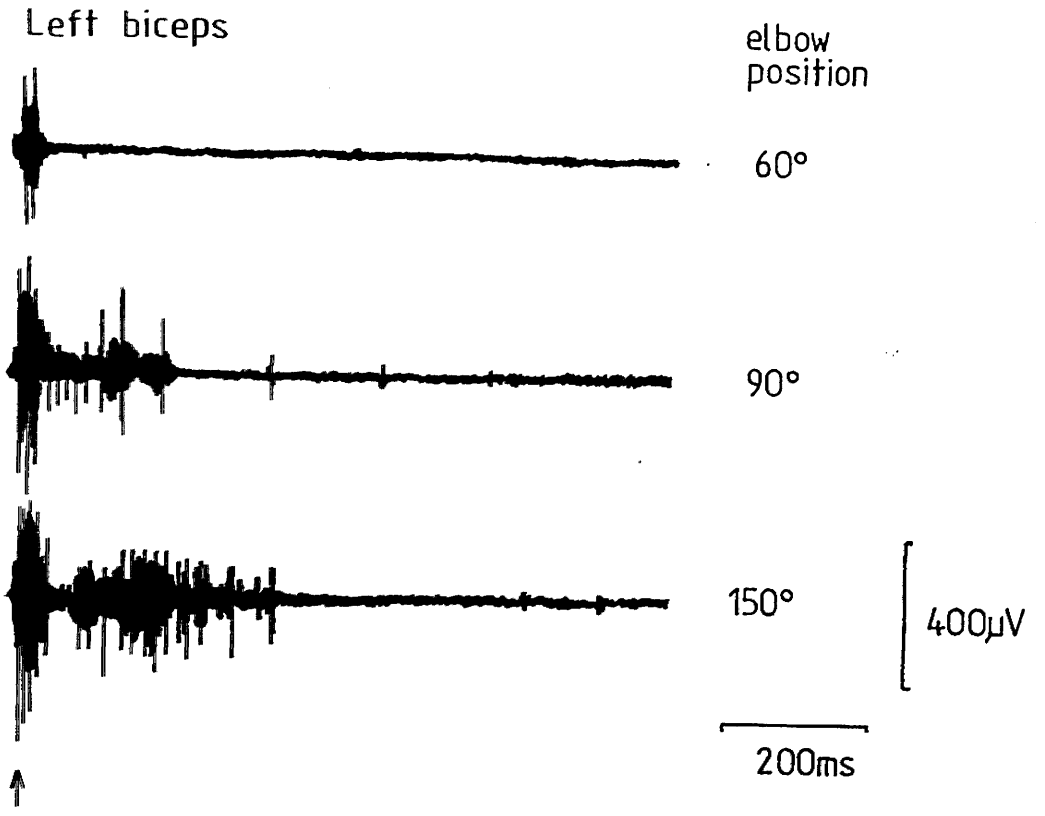


Figure 70. The effect of altering left elbow joint position on flexion reflexes recorded in the left biceps. Electrical stimulation of the dorsal cutaneous branch of the left radial nerve at a fixed intensity was used throughout. Arrows denote the end of the train of stimulus pulses: (decerebrate cat, intact labyrinths, C1 & C2 cut, head and neck held in the mid-position).

reflexes is not the result of temporal influences leading to facilitation or depression as movements of the limb in one direction always acted upon reflex excitability in the same way, while movements to positions in the other direction affected the reflex response in an opposite way. Furthermore, Fig. 71 illustrates the influence of sustained periods of stimulation on the variability of the size of flexion reflexes recorded once every six seconds over a ten minute period at a fixed elbow position (90 degrees) using a fixed stimulus intensity. The stimulus was presented to the left radial nerve and the flexion reflex recorded from the left biceps. Measuring the size of the rectified and integrated EMG response to a fixed stimuli and plotting this as a histogram of reflex amplitude and also with respect to time, the degree of variability between the 100 reflex response can be judged. The histogram shows that the reflex responses appear to be normally distributed, showing neither a tendency to increase or decrease in size. This is also evident from the plot of reflex amplitude against time, which shows the absence of any drift from the mean reflex size. Furthermore as the shape of the distribution appears normal it seems resonable to suggest that the stimulation parameters are such as to discount any temporal influences on reflex size. It would therefore appear that modulation observed by changes in joint position do reflect a genuine somatosensory interaction.

3.5.3 The interaction between limb, head and neck positional influences on extensor reflexes.

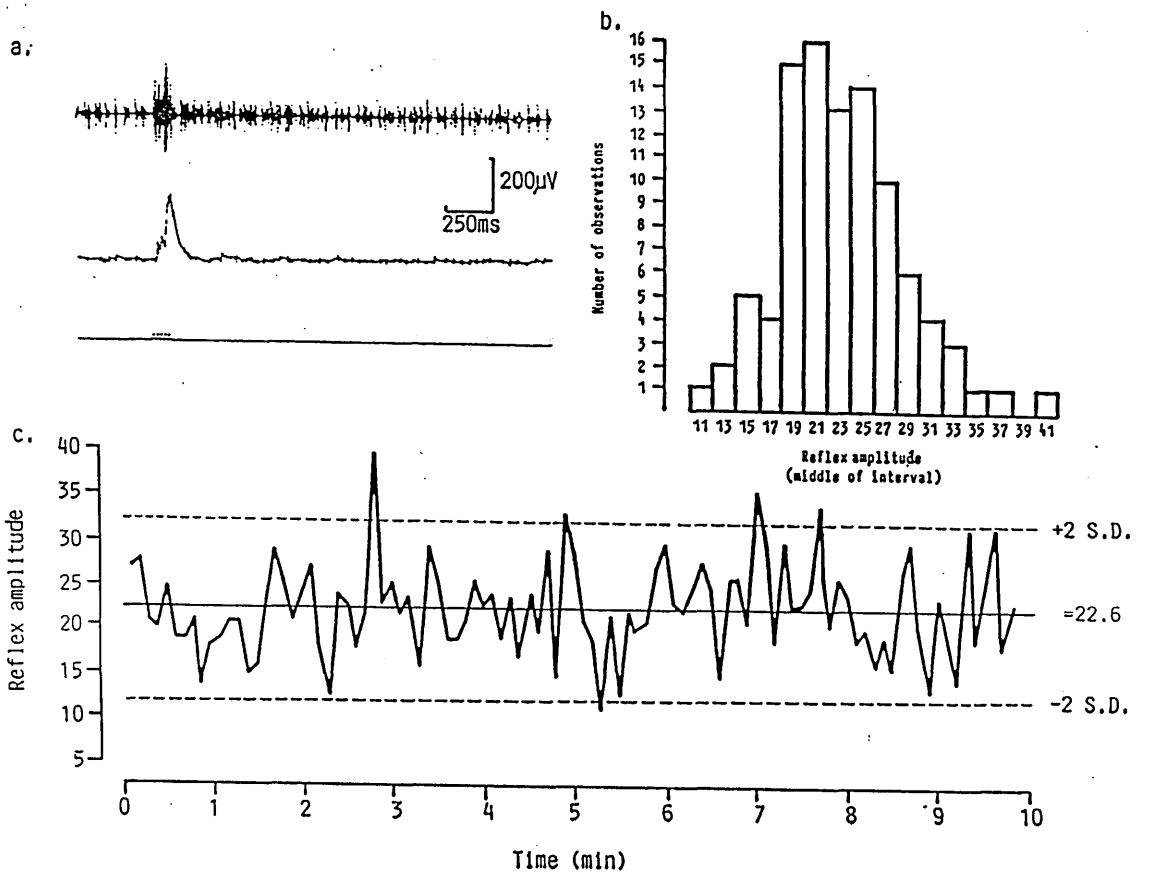


Figure 71. Variability in the size of the flexion reflex with time. (a) Flexion reflex recorded in the left biceps and illustrated as raw EMG and rectified and integrated EMG, stimulus pulses are shown below EMG record. (b) Histogram of variability in reflex amplitude (measured from the area under the rectified and integrated EMG) seen within 100 consecutive reflexes, and recorded over a 10min period (repitition rate once every 6 seconds). (c) Variability of reflex amplitude with time over the 10 min recording period. The stimulus parameters remained constant throughout the series of recordings. (Decerebrate cat, intact labyrinths, C1 and C2 cut, head and neck fixed in the mid-position).

Fixed stimuli presented to the dorsal cutaneous branch of the radial nerve have been demonstrated to result in crossed extensor reflexes that can be modulated independently by changes in elbow and head position. In Fig. 72 changes in head position and elbow position are shown to interact to modify reflexes recorded in the left triceps following electrical stimulation of the right radial nerve. This figure illustrates how changes in head position at different elbow positions modify the reflex response to the fixed stimuli. By looking at each of the vertical columns in Fig. 72 the effect of altering head position at fixed joint positions can be observed, while each horizontal row depicts the influence changes in limb position, at fixed head attitudes, have on the reflex response. Neck position is not altered and remains in the mid position throughout. From the figure it can be seen that at all joint positions, changes in head attitude modulate the crossed extensor reflex, such that when compared to reflexes evoked with the head in the mid position there is a facilitation in the reflex intensity with the head held tilted 30 degrees left side-down, and a depression with the head rotated right side-down. This modulation is evident at the three joint positions illustrated, though it can be seen that if joint position is also considerd, then the greatest facilitation of the crossed reflex occurs when the limb is held in flexion. Thus the combined effect of changing head and elbow position result in the greatest reflex response occurring

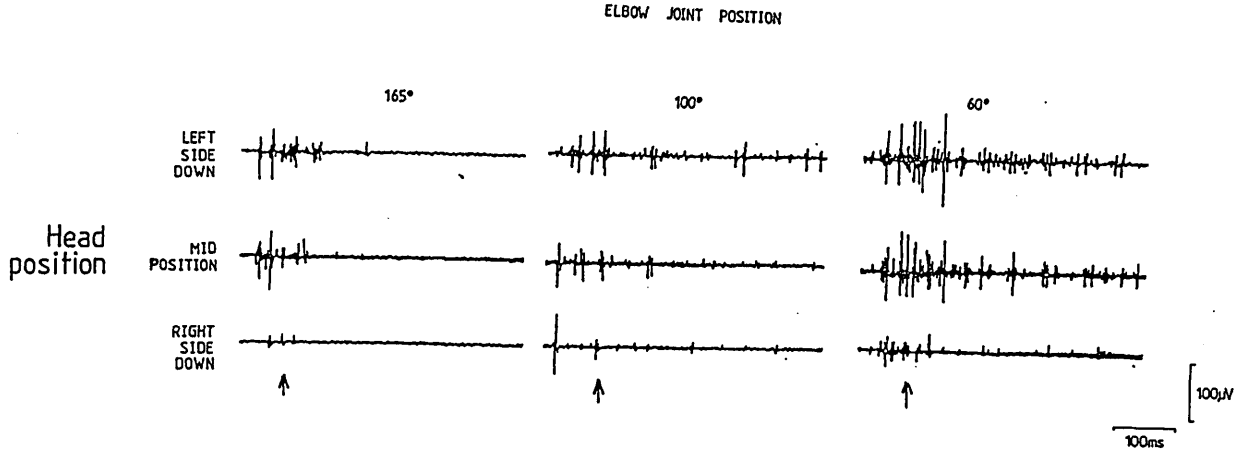


Figure 72. The effect of alteration of head and left elbow joint position on the intensity of the crossed extensor reflex recorded in the left triceps. Electrical stimulation of the dorsal cutaneous branch of the right radial nerve at a fixed intensity was used throughout. The arrows denote the end of the train of stimulus pulses. (Decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

with the head tilted 30 degrees to the left and the limb held at an angle of 60 degrees at the elbow.

Such modulation of the crossed extensor reflex is also evident in the right triceps following the presentation of a fixed intensity of stimuli to the left radial nerve. In this instance the effect of head tilt is opposite to that described for the left triceps in Fig. 72 (and is in agreement with the asymmetry between extensor activity with changes in head position). Thus in the right triceps (as illustrated in Fig. 67) head tilts to the right facilitate the crossed extensor reflex, while tilts left side-down depress the reflex. Consequently, when the position of the right elbow is changed (see Fig. 73) the interaction between the two reflex systems result in modulation of the right crossed extensor reflex such that reflexes are weakest with the head tilted toward the left and the limb fully extended. As in the left limb more flexed positions of the elbow result in facilitation, which in this instance produces the most intense reflex when the limb is held in flexion (60 degrees) and the head rotated 30 degrees to the right. Thus, Figs. 72 and 73 show how changes in limb position can regulate the labyrinthine influence upon extensor reflex output.

In both right (Fig. 72) and left (Fig. 73) forelimbs, the size of the reflex at any one head position increases with flexion while head rotation operates to influence opposite extensor muscles in an asymmetric pattern. Therefore, irrespective of which forelimb is concerned it can be generally concluded, in concerning

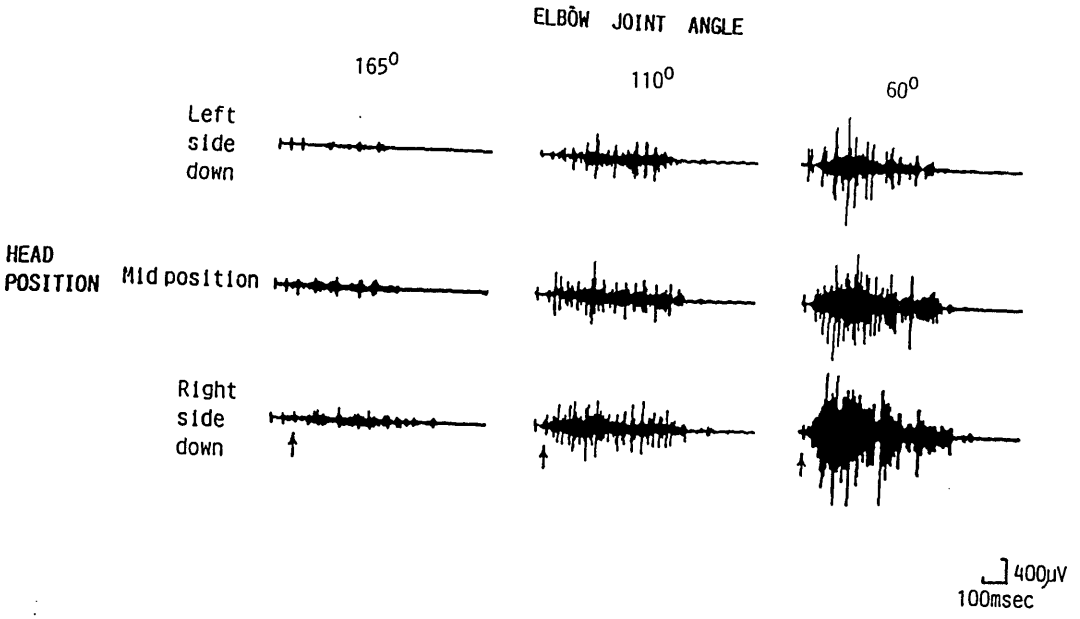


Figure 73. The effect of alteration of head and right elbow joint position on the intensity of the crossed extensor reflex recorded in the right triceps. Electrical stimulation of the dorsal cutaneous branch of the left radial nerve at a fixed intensity was used throughout. The arrows denote the end of the train of stimulus pulses. (Decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

animals with intact labyrinths, that crossed extensor reflexes are greatest with the limb in flexion and the head rotated side-down (with respect to the recorded limb) and are weakest when the limb is extended and the head tilted side-up. At intermediate joint positions there is a continuity of this modulation.

So far only changes in reflex response to alterations in head position have been shown to be regulated by elbow position, in Fig. 74 the effect of altering neck and elbow position on the crossed extensor reflex in right triceps is shown. In this figure head position is maintained at 0 degrees and the axis vertebra rotated from a mid position to positions either 30 degrees left or right with the elbow held in an extended (165 degrees), a mid range (110 degrees) and a flexed (60 degree) position (as with Figs. 72 and 73 a fixed stimulus is used throughout). The figure (74) shows that at all neck positions there is a facilitation of the crossed reflex with movement of the elbow to more flexed positions. At all elbow positions, and in contrast to labyrinthine influences, the neck modulates the reflex response in a manner to produce the greatest response when the neck is rotated to the left (side-up) and the weakest response with the opposite rotation. Consequently, when the limb position is considered along with the neck attitude the resultant integration results in the greatest overall response occurring in the reflex output of extensors when the elbow is flexed and the neck rotated away from the recording site (to the left in Fig. 74). Similarly, the weakest overal

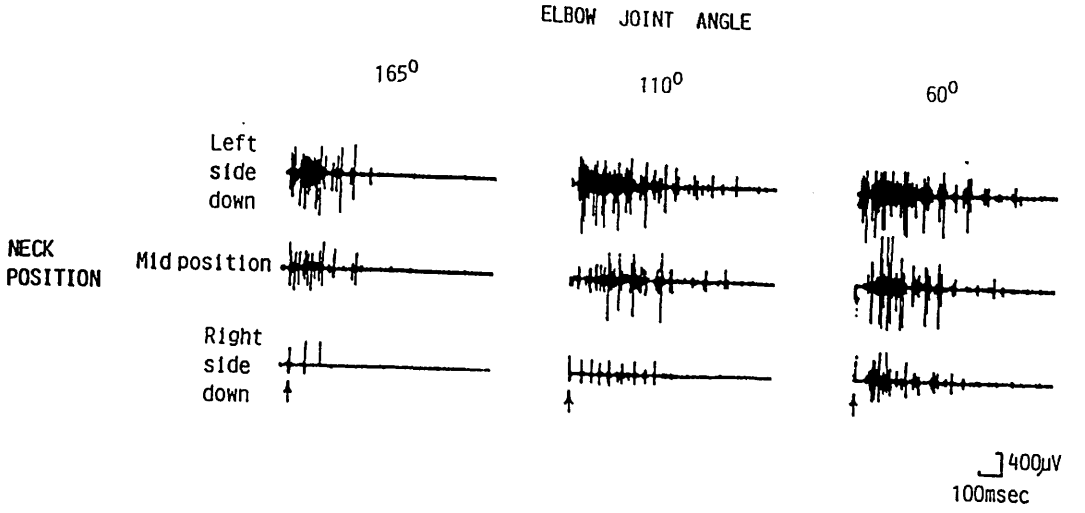


Figure 74. The effect of alteration of neck and right elbow joint position on the intensity of the crossed extensor reflex recorded in the right triceps. Electrical stimulation of the dorsal cutaneous branch of the left radial nerve at a fixed intensity was used throughout. The arrows denote the end of the train of stimulus pulses. (Decerebrate cat, intact labyrinths, C1 & C2 cut, head held in the mid-position).

response is seen to correspond to extended joint positions and neck tilts toward the recording site (to the right in Fig. 74). Compared to labyrinthine influences on extensor output the neck is seen to act in a reciprocal fashion, as can be predicted from studies detailing direct responses observed in forelimb extensors following neck stimulation (Lindsay et al, 1976; Ezure and Wilson, 1983).

The modulation of both labyrinth and neck reflex influences by altering limb position can, as seen in Figs. 72, 73 and 74, greatly influence the size of the reflex output of the extensor muscles. In some instances the crossed extensor reflex can be completely suppressed with changes in limb position. An example of this is illustrated for labyrinth influences to the right triceps in Fig. 75. In this figure the reflexes are represented graphically, the area under the rectified and integrated EMG following the presentation of a stimulus train to the left radial nerve is used as an index of reflex output (the scale used is in arbitrary units). The graph illustrates that, with the stimulus used, no reflex response is recordable at any head position with the elbow fully extended, though at less extended and more flexed positions there are observable reflexes at all head positions. These reflexes show the same pattern of modulation with head and elbow position as illustrated for the right triceps in Fig. 73. The peak in the graph occurring where the interactions between labyrinth and neck influences are at a premium, that is, flexion and head tilted side-down. The demonstration that at a particular joint position there is a complete

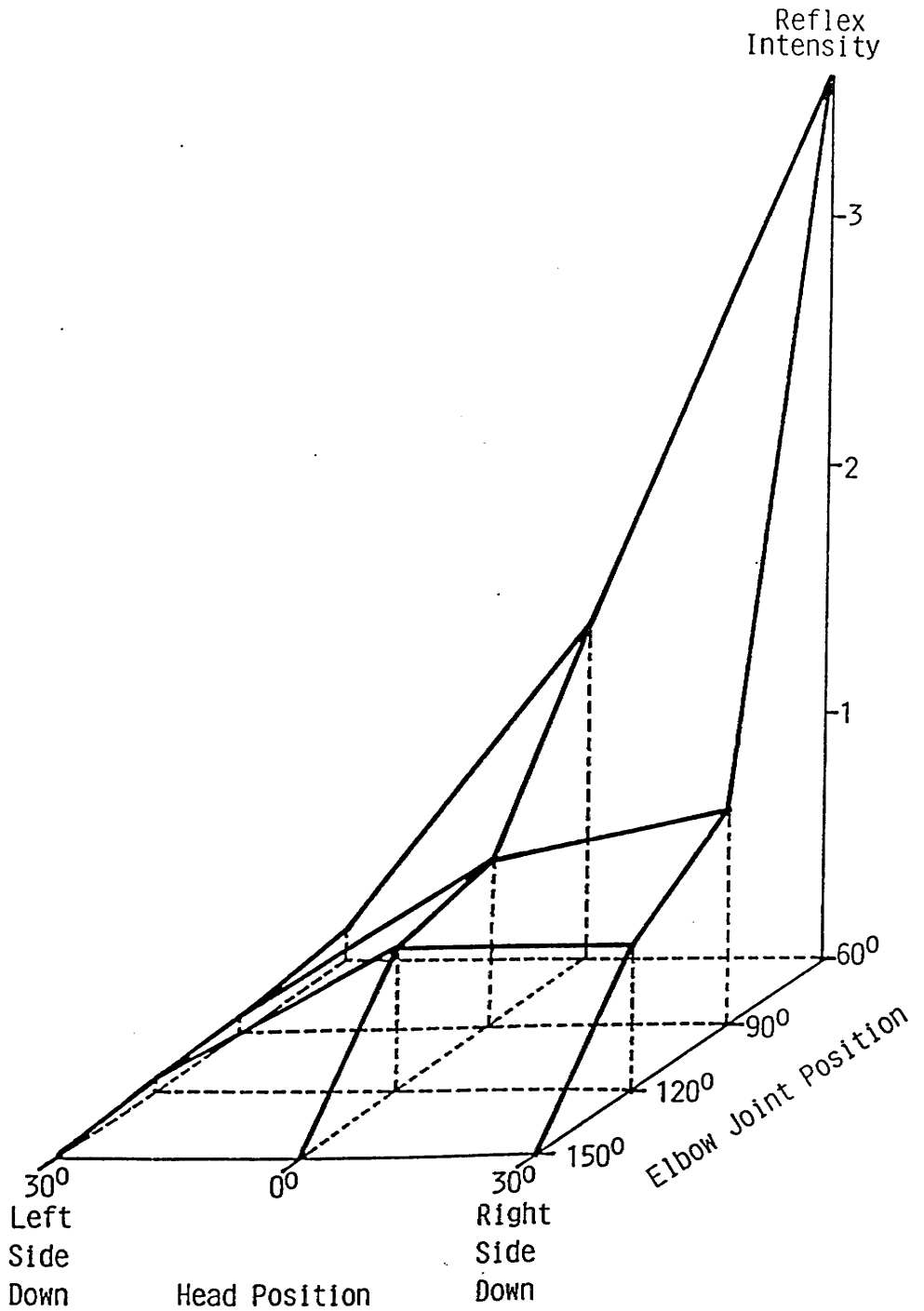


Figure 75. The effect of changing head position and right elbow joint angle on the intensity of crossed extensor reflexes in the right triceps. Reflex intensity was determined from measurements of the area under the rectified and integrated EMG's. An identical train of stimulus pulses were delivered to the dorsal cutaneous branch of the left radial nerve at each combination of conditioning positions. (Decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

suppression of the reflex response to a fixed stimuli at all head positions illustrates the strong influence limb position can have on the crossed extensor reflex.

In addition to the demonstration that limb position influences the conditioning of extensor reflexes by labyrinth and neck proprioceptor systems it was also possible to see interactions between somatosensory and descending influences on flexion reflexes.

3.5.4 The nature of the interaction between labyrinth, neck and limb position on flexion withdrawal reflexes.

Earlier figures have shown that flexion reflexes evoked by ipsilateral stimulation of cutaneous branches of the radial nerve can be influenced independently by changes in head and elbow position. The nature of this conditioning of flexion reflexes from the labyrinth, as has been mentioned previously, is in agreement with the form of labyrinth reflexes described in this thesis, while the influence of limb position on the intensity of flexion reflex is as described by Baxendale and Ferrell (1982). When considered together as a complete system, the form of the interaction bears a close affinity with that seen to affect the extensors. The interactions seen in the flexor responses reciprocating with that observed in the extensors. Fig. 76 illustrates the interaction between labyrinth and limb proprioceptive influences on the intensity of flexion reflexes recorded in the right biceps on electrical stimulation of the right radial nerve at a

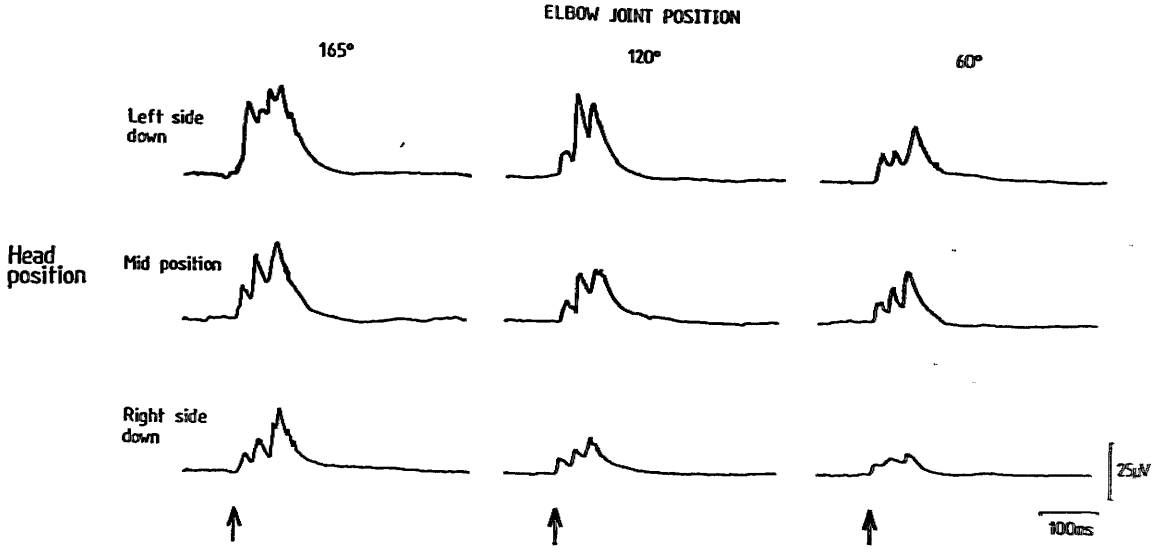


Figure 76. The effect of changing head position and right elbow joint position on the intensity of flexion reflexes in the right biceps. The recorded EMG has been rectified and integrated. The stimulation parameters remained constant throughout the series of recordings. Electrical stimulation was applied to the dorsal cutaneous branch of the right radial nerve. Arrows denote the end of the train of stimulus pulses. (Decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

fixed intensity. The figure illustrates that the nature of the interaction results in conditioning of the flexion reflex such that reflex size is a function of the two distinct afferent inputs. The largest response is observed when the head is left side-down and the limb fully extended. Correspondingly, the weakest reflex response recorded in this muscle (right biceps) was seen with the head rotated right side-down and the limb flexed. Such behaviour contrasts with the behaviour of the right triceps (Fig. 73) during similar testing.

When neck position is altered along with elbow position, the flexion reflexes observed from a flexor from right or left forelimbs show reciprocal changes in intensity to extensor reflexes obtainable from a particular limb. The reflex intensity is modulated by positional changes of the neck and elbow to give the strongest response to a fixed stimulus with the neck side-down and the limb extended. The weakest reflex is evoked when the neck occupies a side-up position and the limb in question is held in flexion.

The conditioning influences onto flexion and extension reflexes, in any one limb, from labyrinth, neck and limb appear strictly organised in relation to each other. Within one limb this organisation reflects the reciprocal pattern of labyrinth reflexes on extensors and flexors, the antagonism between labyrinth and neck reflexes and their dependance on limb position.

In addition to monitoring changes in reflex size to a fixed stimuli, observations were made on the modulation

of reflex threshold with changes in position of the head, neck and elbow. This was done in order to assess if changes in threshold could account for the observed modulation of reflex intensity.

3.5.5 Effect of labyrinth, neck and elbow position conditioning on segmental reflex threshold in the forelimb of cats with intact labyrinths.

The studies detailed above describe changes in reflex intensity associated with changes in head, neck and elbow position. In this section of the thesis a different approach of investigation of limb influences affecting labyrinth and neck reflex effects was employed. Rather than utilizing a fixed stimulus to evoke withdrawal reflexes at combinations of limb, head and neck position the stimulus intensity was gradually increased from zero, at combinations of positions until an intensity was reached that resulted in detectable signs of reflex activity. The intensity evoking these first observable signs of reflex activity was judged to be reflex threshold.

Crossed extensor reflexes recorded in the triceps muscles of the forelimb show intensity variations that are dependant on the position of the head, neck and elbow. Such changes can also be seen in measurements of reflex threshold. Fig. 77 gives an example of how crossed extensor reflex threshold alters with changes in head and elbow position (Fig. 77a), and neck and elbow position (Fig. 77b). In both Fig. 77a and b the reflex was recorded from

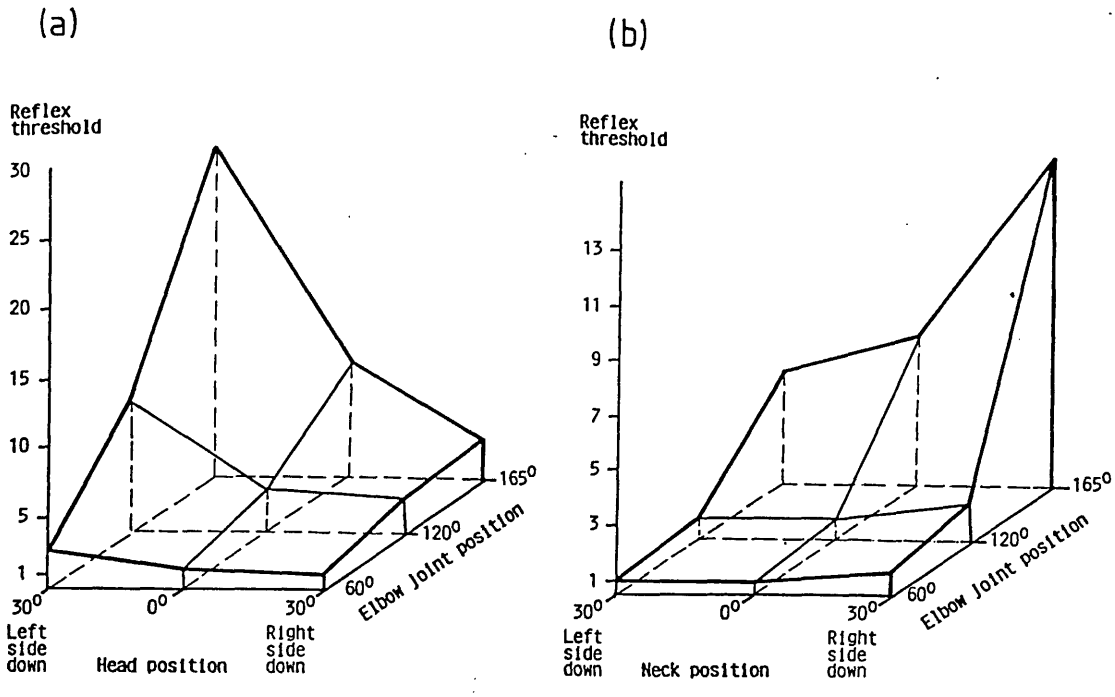


Figure 77. The effect on the threshold of the crossed extensor reflex in the right triceps on changing, (a) head and right elbow joint position, and (b) neck and right elbow joint position. Reflex threshold is expressed as a multiple of the minimum intensity required to elicit the reflex at any combination of conditioning positions of the head, neck or forelimb. Electrical stimulation of the dorsal cutaneous branch of the left radial nerve was used. In (a) neck position was fixed in the mid-position, while in (b) head position was not altered from the mid-position. (Decerebrate cat, intact labyrinths, C1 & C2 cut).

the right triceps. The modulation seen in Fig. 77a is comparable to that seen in Fig. 73 in which reflexes were evoked using a fixed stimuli. With changes in head position Fig. 77a shows that reflex threshold at any particular joint position is modulated such that threshold is lowest with the head held right side-down and highest with head tilts left side-down. Similarly threshold modulation with joint position at any particular head position reveals that threshold is lowest with the elbow flexed (60 degrees), and is highest when fully extended (165 degrees). Consequently, when both changes in head and elbow position are considered threshold is modulated so that the reflex in the right triceps is most easily evoked with the limb flexed and the head tilted right side-down, while it is most difficult to evoke when the head is tilted left side-down and the left limb held in extension. The 3-D representation of this modulation shows that at intermediate positions there is continuity in the modulation, such that a surface can be constructed which rises from the position of lowest threshold to that where threshold is at a maximum. It can therefore be envisaged that the changes in reflex intensity observed in the crossed extensor reflex of the right triceps and resulting from head and elbow positional changes (Fig. 73) are a consequence of the alterations in the reflex threshold. Similarly, changes in reflex intensity with changes in neck and elbow position (Fig. 74) can also be seen to correspond with changes in the reflex threshold as illustrated in Fig. 77b. As both Fig. 77a and b are obtained from the right triceps the antagonism

between labyrinth influences on one hand, and neck influences on the other, can be seen. With neck rotations, the threshold for the crossed extensor reflex in the right triceps is greatest when the axis vertebra is rotated to the right and the right forelimb extended. Reflex intensity is at its lowest when the limb is flexed and the neck tilted left side-down. This form of modulation resulting in a graph, which in comparison to that showing head-elbow threshold modulation is orientated such that all points on the neck position axis have opposite gradients to equivalent points on the head position axis of Fig. 77a.

As the labyrinth and neck show antagonistic influences on the crossed extensor reflex in the same limb it can be envisaged from these figures (Fig. 77a and b) that the crossed reflex threshold is affected by labyrinth and neck reflex systems in an asymmetric manner. It can therefore be generally stated that side-down tilts of the head, as defined with respect to the recording site, result in a lowering of threshold while side-up tilts increase reflex threshold in elbow extensors, while changes in neck position, as described earlier, oppose these actions. In addition to these asymmetric influences acting on opposite limbs from labyrinth or neck stimulation one can add the ipsilateral joint position dependant threshold modulation, which has a common action on the reflex of the limb involved.

As with the normal pattern of labyrinth and neck reflexes seen in cats with intact labyrinths the flexor musculature also shows changes in reflex threshold that

reflect the conditioning influences from the labyrinth and neck. In the case of flexion reflexes these effects are reciprocally organised to the threshold changes seen in extensor reflexes.

Considering the influence of the labyrinth on the threshold of flexion reflexes, and also the effect of changing limb position it can be seen from Figs. 78 and 79, which represent threshold modulation in right and left elbow flexors (biceps), that reciprocal changes in flexion reflex threshold can be recognised in relation to; (1) each limb (compare Fig. 78 to 79), (2) labyrinthine conitioning between extensor and flexor of a particular limb (compare Fig. 77a to 78) and (3) between the joint position dependant conditioning influence on extensor and flexor reflexes in a particular limb (compare Fig. 77a with 78).

Fig. 78 shows the modulation of flexor reflex threshold in right biceps with changes in head and elbow position. [This figure is drawn in such a way as to conform with the layout of other 3-D representations of threshold modulation. As a consequence of the form of the modulation the reader may have difficulty in visualising the shape of the graph. It is hoped that the shading will facilitate this. Additionally as a further aid a 2-dimensional graph has been inserted that illustrates the same data.] This figure demonstrates that threshold changes seen with rotations of the head reflect the influence seen from labyrinthine receptors on the behaviour of flexion reflexes evoked via fixed stimuli in this muscle (cf. Fig. 76). Head tilts to the right (ie. side-down) result in an increased

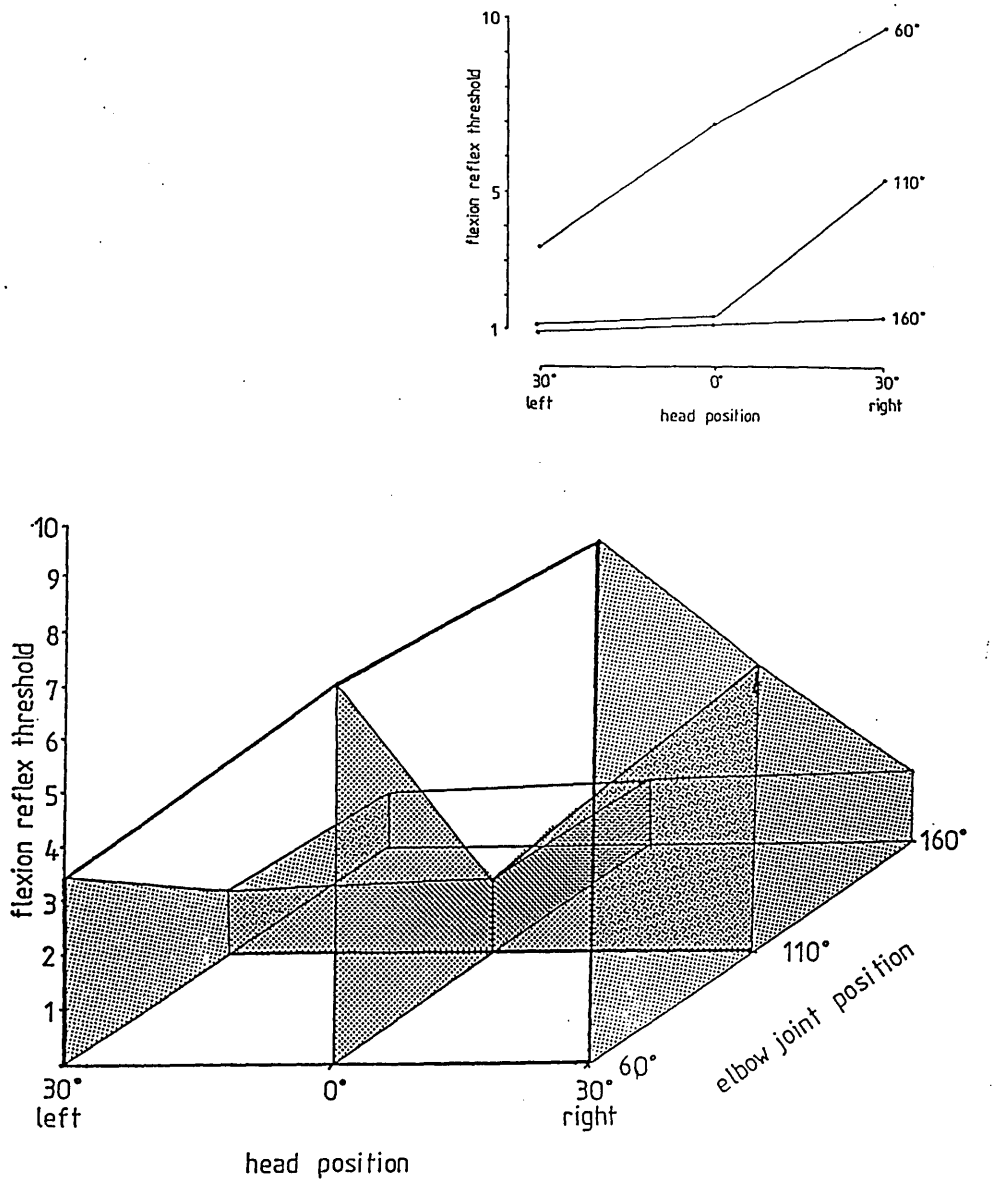


Figure 78. The effect on the threshold of the flexion reflex in the right biceps on changing head and right elbow position. Reflex threshold is expressed as a multiple of the minimum intensity required to elicit the reflex at any combination of head and elbow position. Both graphs depicted in this figure illustrate the same data. Electrical stimulation of the dorsal cutaneous branch of the right radial nerve was used. Neck position was maintained in the mid-position throughout the period of testing. (Decerebrate cat, intact labyrinths, C1 & C2 cut).

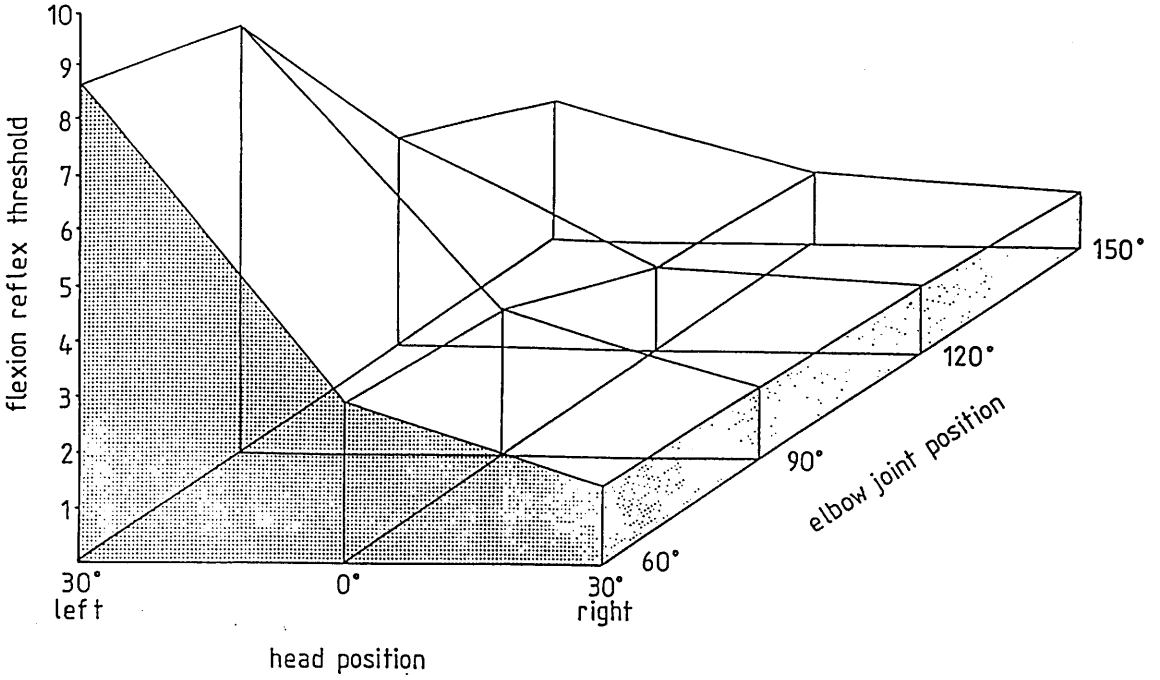


Figure 79. The effect on the threshold of the flexion reflex in the left biceps on changing head and left elbow joint position. Reflex threshold is expressed as a multiple of the minimum intensity required to elicit the reflex at any combination of head and elbow position. Electrical stimulation of the dorsal cutaneous branch of the left radial nerve was used. Neck position was maintained in the mid-position throughout the period of testing. (Decerebrate cat, intact labyrinths, C1 & C2 cut).

reflex threshold, those to the left result in a reduced flexion reflex threshold. In addition, modulation occurs with changes in limb position so that when considered together, the threshold of the flexion reflex becomes a function of head and elbow position. The direction of modulation with limb position is such that there is an overall increase in threshold at each head position as more flexed limb attitudes are attained. In association with this, the modulation becomes deeper with more flexed joint angles.

The relationship described above for the modulation of flexion reflex threshold in the right biceps is also apparent in the reflex behaviour of the left biceps, (Fig. 79). Fig. 79 differs from Fig. 77 in respect to the effect head position has on the reflex threshold. The threshold at any particular joint position is lowest when the head is tilted to the right, as compared to the left in Fig. 78, and similarly, threshold is greatest when the head is rotated to the left rather than the right. The two figures demonstrate that the labyrinthine influences onto flexor reflex pathways on opposite sides of the animal are reciprocally organised. Furthermore, as joint angle can be seen from Figs. 78 and 79 to influence reflex threshold independently and has the same directional influence irrespective of the limb involved it can be seen that qualitatively the form of the surfaces defined in these two figures are reflections of each other in a vertical plane defined as parallel to the joint position axis and intersecting the head position axis at zero degrees. Thus

the results from the flexor of one limb can be thought to reflect changes that would occur in the opposite side through a simple transformation.

Similarly, though again in qualitative terms, the surface outlined by the flexion reflex threshold in the right limb appears as a translation of the surface defined for the extensor reflex modulation in that limb (Fig. 77a). The translation in this relationship being of the form of a reflection of each point in a vertical plane passing through coordinates defined at the following points; (head tilted left side-down, limb flexed), (head tilted right side-down, limb extended). This translation (or transposition) revealing that two reciprocal relationships operate on the organisation of flexor and extensor reflexes and that these relationships under labyrinthine and limb proprioceptor control act antagonistically on each of these reflexes. Appendix B defines a set of elementary operations that summarize these reciprocal relationships.

As Fig. 77 expressed the antagonism between labyrinth and neck conditioning on extensor reflexes, Fig. 80 illustrates the predicted antagonism resulting from these sources on the magnitude of flexion reflex threshold in the right biceps. The graph illustrates two sets of threshold measurements obtained at two differnt elbow joint angles (90 and 120 degrees). At each of these joint positions it is clear that changes in head or neck position result in opposing influences on flexion reflex threshold. As in Fig. 78 the threshold is increased with head rotations to the right and decreased when the tilt is

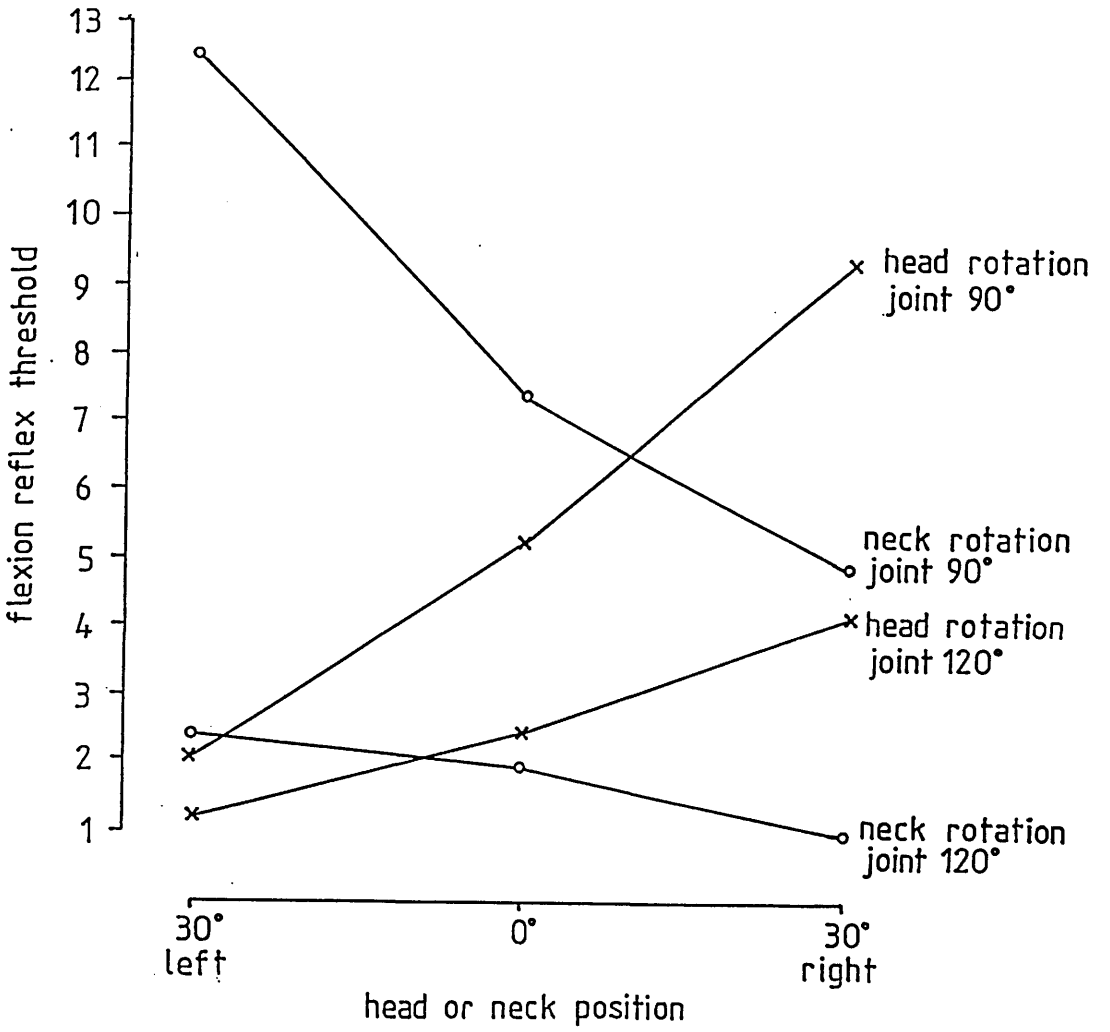


Figure 80. Graph depicting the antagonism between labyrinth and neck conditioning influences on the threshold of the flexion reflex in the right biceps at two different right elbow joint positions. Reflex threshold is expressed as a multiple of the minimum intensity required to elicit the reflex at any combination of conditioning positions of the head, neck or forelimb. Electrical stimulation of the dorsal cutaneous branch of the right radial nerve was used. (Decerebrate cat, intact labyrinths, C1 and C2 cut).

directed towards the left. Positional changes of the limb also alter threshold, this influence acting in the same direction as shown to occur in Fig. 78, flexion of the limb increasing threshold and extension reducing it.

Together the figures illustrated in this section show that the threshold of flexion and extension reflexes can be influenced from the labyrinth, neck and the limb itself. The change in threshold measurements complimenting the results showing modulation of reflex intensity with various conditioning influences, and show that a set of specific relationships exist that govern the responses observed. The behaviour of segmental reflexes revealing trends in the pattern of convergence and interaction of influences derived from head, neck and elbow position.

3.5.6 The possible receptor origin of the reflex modulation observed to arise from the limbs.

Changes in limb position, as used in these experiments, require change in the angle of the limbs only at the elbow (see methods). Any change in limb position about the elbow will necessarily alter the length of muscles that act around this joint. It is therefore necessary, in order to identify the receptor source of this modulation of reflex intensity and threshold, to consider if these changes in length contribute via muscle receptors to the results described above. In an attempt to do this, anaesthetic (lignocaine) was injected into the elbow joint capsule. This procedure is known to block elbow joint

afferent discharge but not interfere with muscle receptor output from surrounding tissues. The introduction of the anaesthesia abolishes the modulation of reflex intensity and threshold with changes in limb position, but does not disrupt the reflex modulation from other sources.

The loss of intensity modulation with alterations in limb position is shown in Fig. 81. The figure illustrates crossed extensor reflexes recorded from the right triceps and evoked using identical stimulus trains at three different joint angles. Head and neck occupy the mid position in this example. In comparison with Fig. 69 in which limb position can be seen to influence the crossed extensor reflex there is no obvious sign of modulation associated with the changes in limb position. It would therefore seem to be that despite altering the length of the muscles in question the positional change now results in no reflex modulation. The implication from this is that the results discussed earlier are independent of stretch reflex mechanisms and that joint afferent activity is required for effective reflex modulation with limb position. That this is also true for changes in reflex threshold can be seen from Fig. 82.

In Fig. 82 the modulation of crossed extensor reflex threshold by changes in head and elbow position are plotted before and after injection of lignocaine (0.5ml) into the joint capsule. The results pertain to the right triceps. Prior to the injection the results correlate well with those illustrated in Fig. 77a for the same test in a different cat. However, following the injection the shape

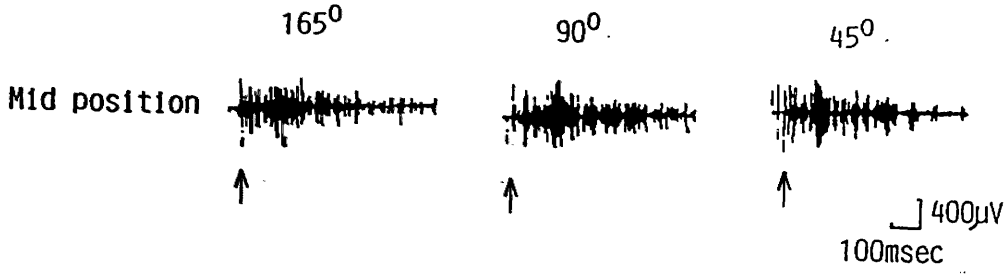


Figure 81. The effect of changing elbow joint position on the intensity of the crossed extensor reflex in the right triceps after injection of a 0.5ml solution of lignocaine (2%) into the synovial cavity of the right elbow joint. The head and neck are maintained in the mid-position throughout. A fixed intensity of electrical stimulation was applied to the dorsal cutaneous branch of the left radial nerve, the end of the stimulus train is denoted by the arrows. (Decerebrate cat, intact labyrinths, C1 & C2 cut).

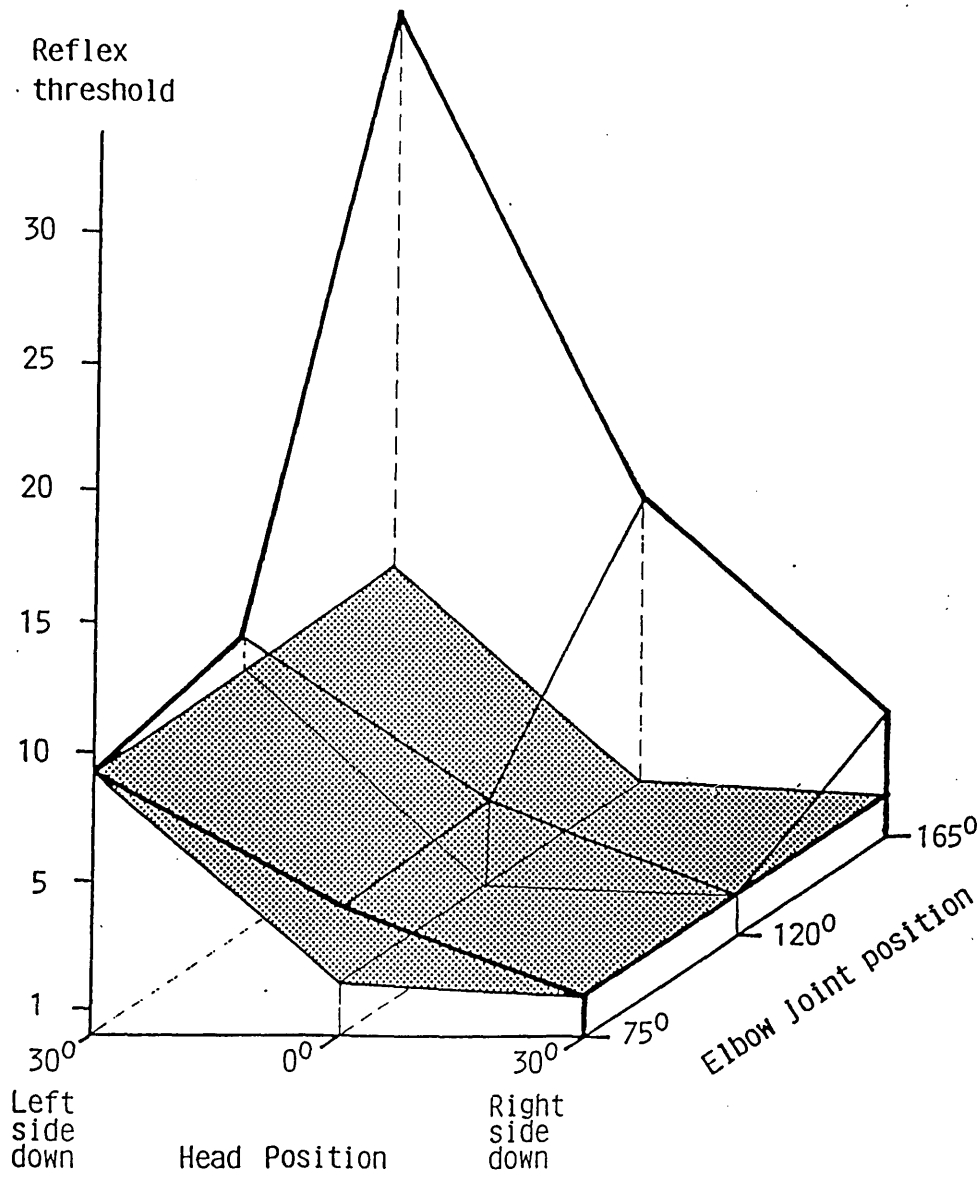


Figure 82. The effect of injection of 0.5ml of 2% lignocaine into the synovial space of the right elbow joint on the modulation of crossed reflex threshold in the right triceps with changes in head and elbow position. The upper 'surface' shows the interaction of labyrinth and elbow joint conditioning inputs prior to the injection of lignocaine, while the lower shaded 'surface' was obtained after the injection. Reflex threshold is expressed as a multiple of the minimum intensity required to elicit the reflex at any combination of conditioning positions of the head and elbow. (Decerebrate cat, intact labyrinths, C1 & C2 cut, axis vertebra clamped).

of the graph is altered considerably. (The stippled area represents the surface defined by the threshold measurements made after joint anaesthesia. It should be noted that the threshold measurements are expressed as multiples of the lowest intensity of stimulus required to evoke a reflex response and that the absolute value of this stimulus was the same before and after joint anaesthesia.)

Local anaesthesia of the joint capsule has effectively abolished the reflex modulation which accompanied changes in elbow position. Threshold measurements at any one head position remain unaltered with limb positional changes. Changes in head position, however are still capable of modulating reflex threshold. This modulation is now seen to be independent of limb position and as such has resulted in an overall reduction in threshold at all head positions. This reduction is most obvious at 165 and 120 degrees. From this it appears that by removing the joint afferent discharge the modulation from labyrinthine influences onto crossed extensor reflex pathways approaches that seen with the limb flexed prior to joint anaesthesia. Thus it would seem that at more extended positions there has been a loss of some inhibitory input, so that a reduction in threshold becomes apparent. That threshold is reduced, implies that the excitability of the reflex system has increased therefore it is difficult to imagine that the lignocaine, through being taken up via the joint circulation has had a central depressant effect.

On injecting anaesthetic into the joint not only were reductions in threshold observed with crossed extensor

reflexes but also ipsilateral flexion withdrawal reflexes. However, whereas extensor reflex threshold after anaesthesia at all joint angles approached threshold values gained previously (before lignocaine injection) with the limb in flexion, the flexion reflex thresholds approach values obtained when extended positions were monitored. Thus anaesthesia affects crossed extension and ipsilateral flexion reflexes in opposite ways but acts so that post anaesthesia values for threshold approach the lowest values seen prior to the injection, coresponding to threshold measurements made with the limb flexed for extensor reflexes and extended for flexion reflexes.

In several animals following succesful completion of a run of threshold measurements, injection of anaesthesia into the joint resulted in the animal becoming more excitable (as in agreement with the results just described). However, it was often the case that this increase in excitability resulted in an unstable background on which to make threshold measurements with any degree of accuracy. What was apparent was that extensor and flexor reflexes could be evoked by using stimuli less intense than was required prior to injection, though it was often the case that a change in excitability would occur prior to the completion of a run of tests. It was also noticed that changes in head or neck position would evoke recordable reflexes themselves, whereas prior to anaesthesia no detectable EMG changes were seen on head or neck tilt. Thus under these circumstances it was difficult to obtain repeatable measurements at combinations of head, neck and

elbow position. It is therefore only possible to gain a subjective rather than quantitative impression from these examples, but in all cases it was apparent that joint position following anaesthesia had no effect on reflex intensity or threshold so long as a stable background was maintained.

3.6.0 Limb positional influences on labyrinth and neck conditioning of protective reflexes in left hemilabyrinthectomized cats.

In previous sections the pattern of labyrinthine and neck reflexes recorded in the acute hemilabyrinthectomized cat have been described. It is the object of this section to strengthen these observations by examining conditioning influences from the remaining labyrinth and from the neck on extension and flexion reflexes in both forelimbs, and in addition to examine if joint position is effective in modulating these reflexes.

3.6.1 Modulation of crossed extensor reflexes in the forelimbs of the acute cat.

Crossed extensor reflexes in cats with intact labyrinths show modulation in intensity and threshold that is dependant on combinations of head, neck and elbow position. In the normal cat this modulation reflects the facilitatory influences from the labyrinth and neck. On destruction of one labyrinth (left side) there is a change

in the organisation of labyrinth reflexes recorded from forelimb extensors.

In the left triceps the labyrinth reflex is not altered following left labyrinthectomy. In the following figures it will be demonstrated that when no apparent reflex activity accompanies a head tilt that a conditioning influence from the labyrinth and neck is evident onto crossed extensor reflex pathways, and that this conditioning is consistent with the reflex pattern observed directly in these muscles. Limb positional information will also be demonstrated to be of importance in modulating these reflexes, and it will be shown that the limb acts as in the normal preparations.

[As described in the section on limb influences in normal cats the results from this section were also obtained from animals that during the course of an experiment entered a state of excitability from which no direct reflexes could be observed following head or neck rotation. In acute animals prolonged reflex testing and conditioning would inevitably result in an excitability change which would compromise complete evaluation of reflex modulation. For this reason only a limited number of tests could be completed without changes in background activity. These incomplete examples conform with the results drawn from examples where levels of excitability were stable long enough to complete a series of tests.]

Electrical stimulation of the right radial nerve with a fixed stimulus train results in crossed extensor reflexes in the left triceps that are dependant on head,

neck and elbow position. In Fig. 83 reflexes from the left triceps are shown that reflect this dependance. With changes in head position (Fig. 83a) reflex intensity is altered in a specific manner. Rotations of the head to the left increase the size of the reflex while rotations to the right reduce it when compared to that obtained in the mid position. Conversely, neck rotations (Fig. 83b) act in the opposite direction, thus in the left limb the modulation of extensor reflexes shows the normal pattern of conditioning despite the loss of the ipsilateral labyrinth. Similarly, the effects seen with changes in limb position also conform with that seen in normal cats. This is illustrated in Fig. 84 and is directly comparable to Fig. 72 obtained from a normal animal. In this figure (84) the positional influence from the limb is seen to modulate the conditioning from the labyrinth such that the largest reflexes are seen in flexion and the weakest in extended limb positions.

The loss of the left labyrinth does not appear to affect conditioning of left extensor reflexes, though in the right limb the pattern of extensor modulation does not conform to the normal pattern. Fig. 85 illustrates the variations in the size of the crossed extensor reflex in right triceps with changes in head and elbow position. Comparison with Fig. 73, where the same tests are carried out on a normal animal, clearly highlight that although joint position dependant modulation is in the same direction there is a reversal in the conditioning influence from the labyrinth. The figure takes the same form as that obtained for the left triceps (Fig. 84) due to this

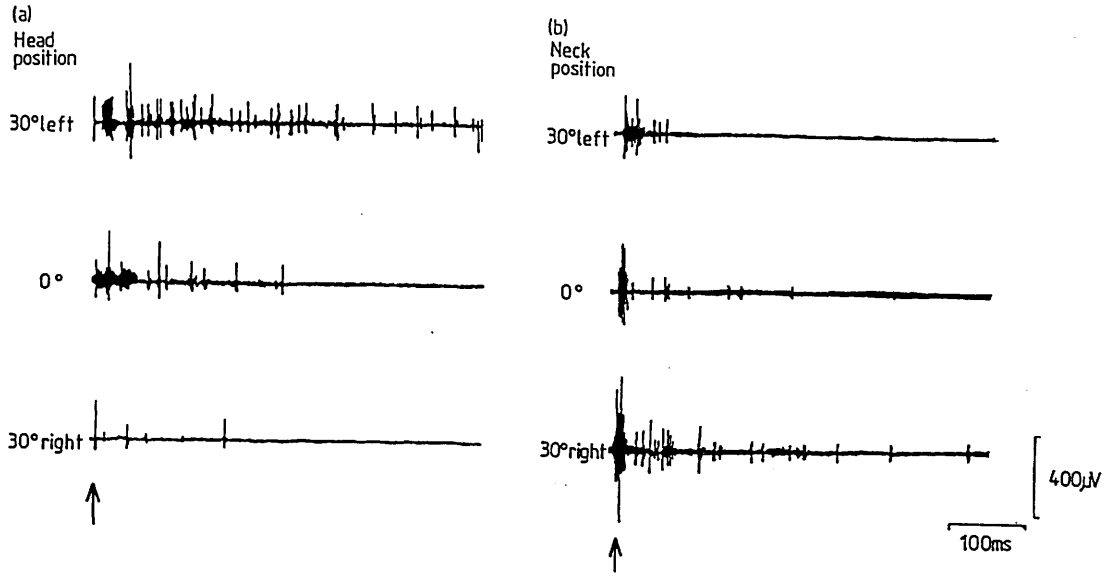


Figure 83. The modulation of crossed extensor reflex intensity in the left triceps with changes in (a) head position and (b) neck position in an acutely hemilabyrinthectomized cat. A fixed intensity of stimulation was applied to the dorsal cutaneous branch of the left radial nerve throughout. The arrows denote the end of the train of stimulus pulse. In (a) the neck was fixed in the mid-position, while in (b) the head was fixed in the mid-position. (Decerebrate cat, left hemilabyrinthectomy carried out immediately prior to decerebration, C1 & C2 cut).

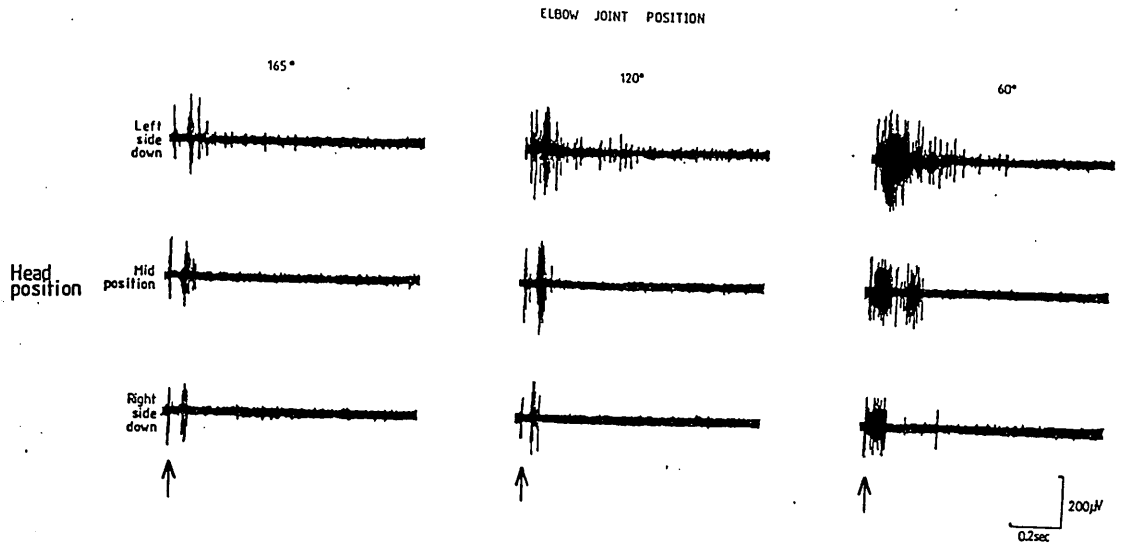


Figure 84. The effect of changing head and left elbow joint position on the intensity of the crossed extensor reflex recorded in the left triceps of an acutely hemilabyrinthectomized cat. Electrical stimulation of the dorsal cutaneous branch of the right radial nerve at a fixed intensity was used throughout. The arrows denote the end of the train of stimulus pulses. (Decerebrate cat, left hemilabyrinthectony performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

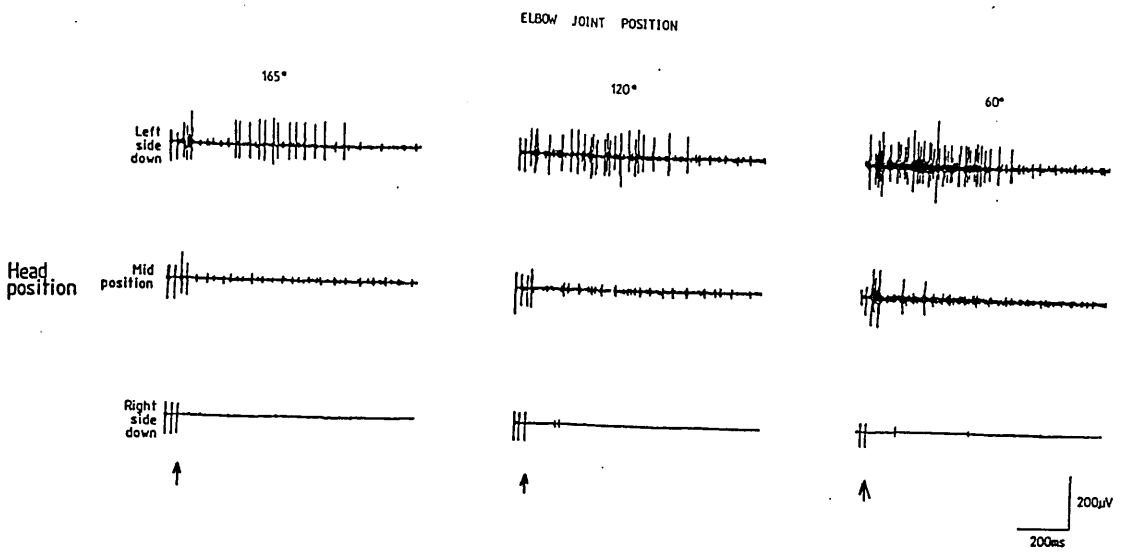


Figure 85. The effect of changing head and right elbow joint position on the intensity of the crossed extensor reflex recorded in the right triceps of an acutely hemilabyrinthectomized cat. Electrical stimulation of the dorsal cutaneous branch of the left radial nerve at a fixed intensity was used throughout. The arrows denote the end of the train of stimulus pulses. (Decerebrate cat, left hemilabyrinthectony performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

reversal in labyrinthine conditioning. Fig. 85 paralleling actions normally associated with neck rotation in the right limb in both normal (Fig. 74) and acute (Fig. 86) preparations. Thus in terms of interactions between labyrinth and neck reflexes the normal antagonism is replaced in the right limb by conditioning influences that act in the same direction (ie. head rotations to the right depress the crossed extensor reflex as do neck rotations in the same direction).

The reversal of the labyrinth influence on the crossed extensor pathway is also evident when changes in reflex threshold are considered. Threshold measurements (Fig. 87) show parallel changes to those seen in reflex intensity. The threshold lowering with head tilts toward the left and increasing on head rotations to the right. The graph describing these threshold changes, as well as those associated with changes in limb position (Fig. 87) has its peak in the opposite corner to that seen for the same limb in cats with intact labyrinths (Fig. 77a). The modulation of right crossed extensor reflexes in left hemilabyrinthectomized cats with changes in head and elbow position resembling that depicted to occur with neck rotations in normal cats (Fig. 77b). Another example of this, which emphasizes that following hemilabyrinthectomy head and neck tilts act in a similar fashion (regarding their conditioning influence) is shown in Fig. 88. In this figure threshold measurements in the right triceps were made following head or neck rotations at one elbow joint angle. In comparing individual measurements from this

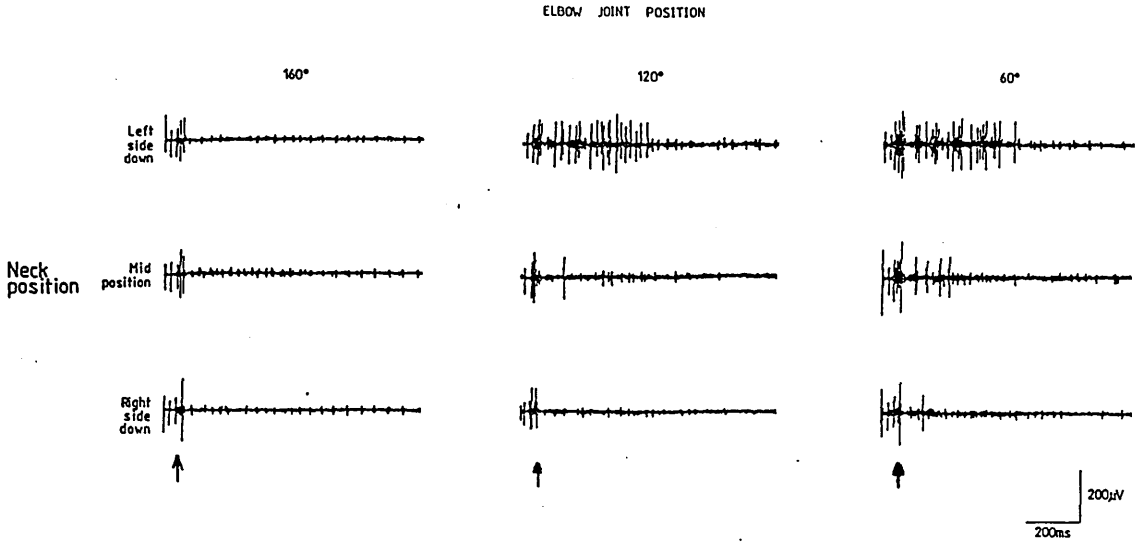


Figure 86. The effect of changing neck and right elbow joint position on the intensity of the crossed extensor reflex recorded in the right triceps of an acutely hemilabyrinthectomized cat. Electrical stimulation of the dorsal cutaneous branch of the left radial nerve at a fixed intensity was used throughout. The arrows denote the end of the stimulus train. (Decerebrate cat, left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, head fixed in the mid-position).

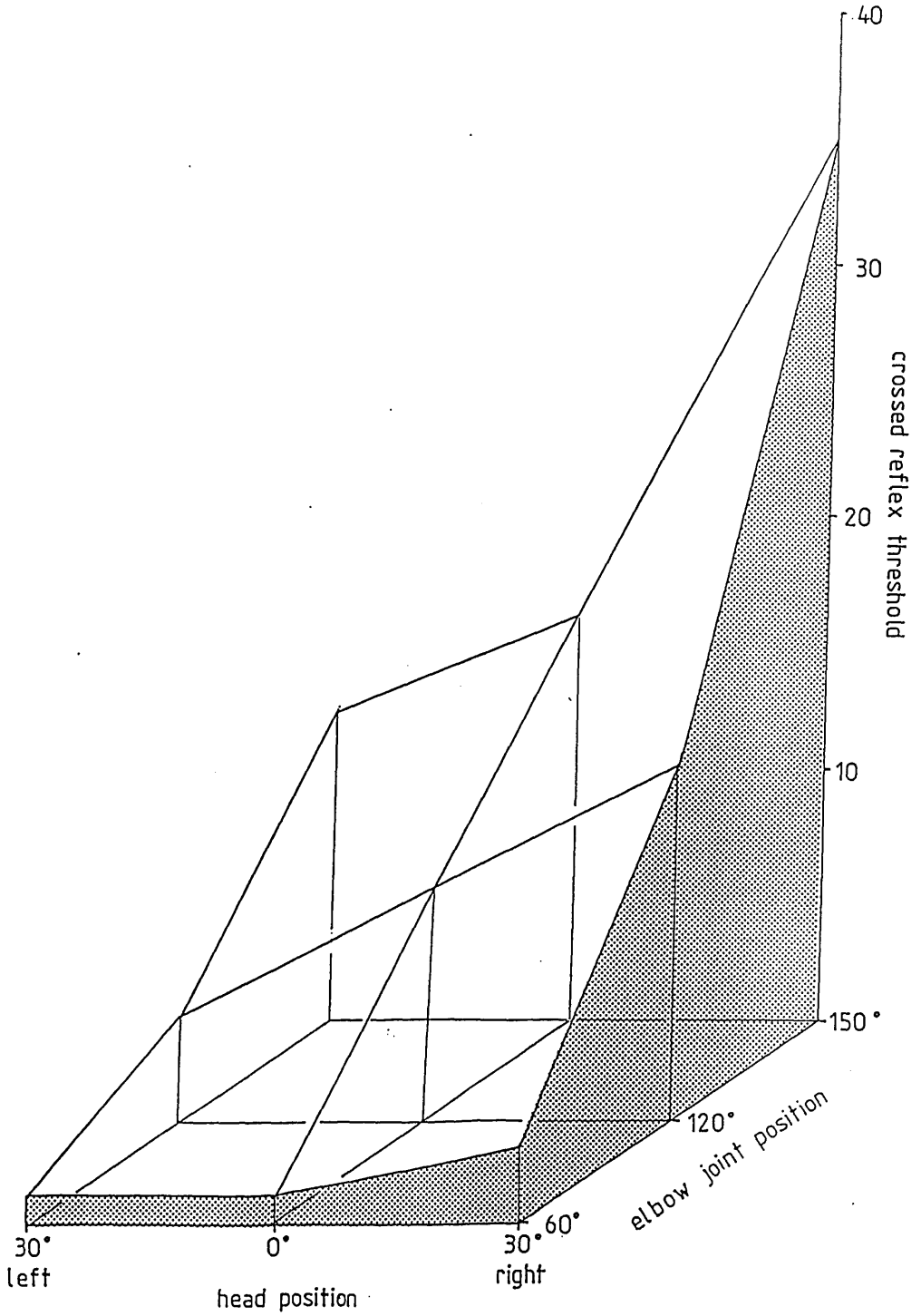


Figure 87. The effect on the threshold of the crossed extensor reflex in the right triceps on changing head and right elbow joint position in an acutely hemilabyrinthectomized cat. Reflex threshold is expressed as a multiple of the minimum intensity required to elicit the reflex at any combination of head and elbow position. Electrical stimulation of the dorsal cutaneous branch of the left radial nerve was used. (Decerebrate cat, left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

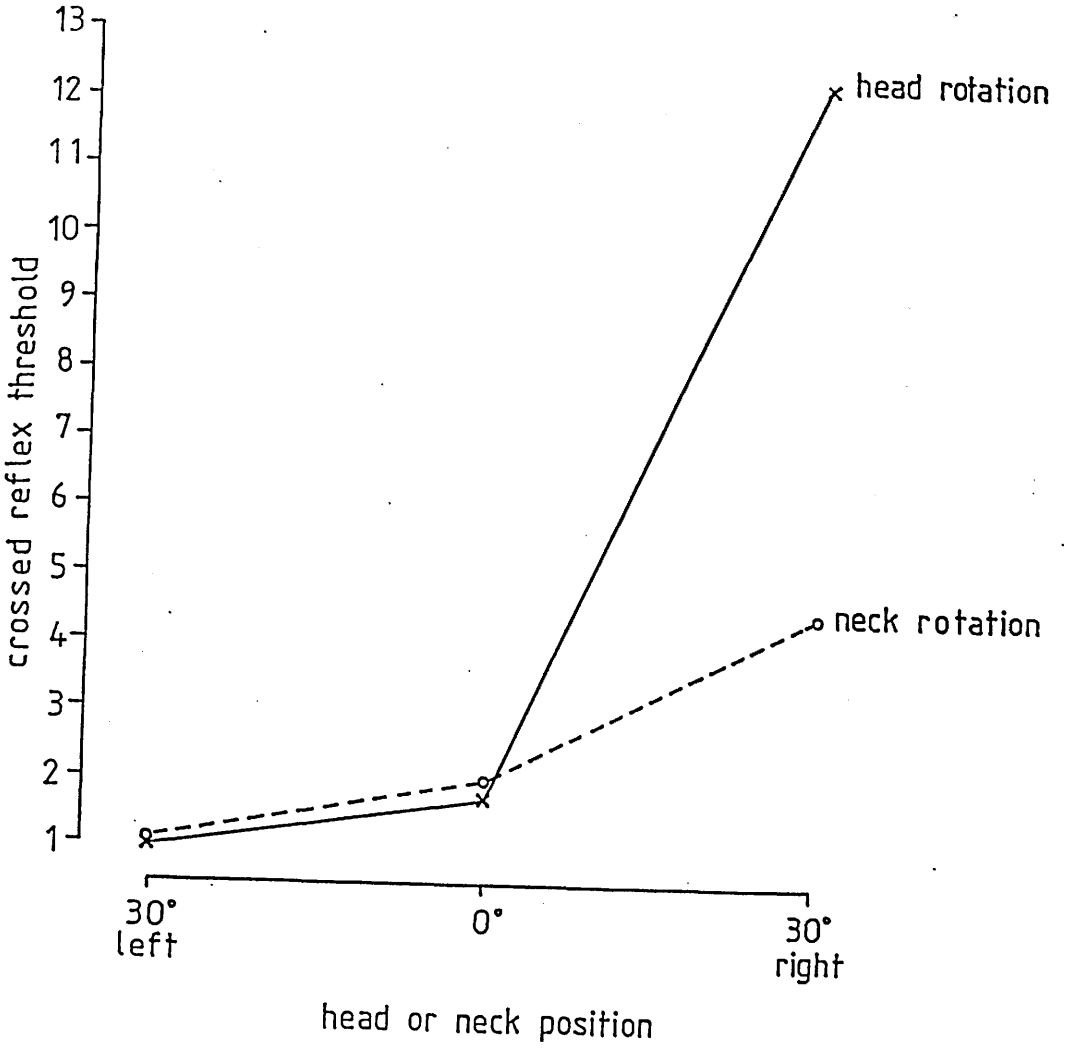


Figure 88. Graph illustrating the independant modulation of crossed extensor reflex threshold by head and neck position in the right triceps of an acutely hemilabyrinthectomized cat. Reflex threshold is expressed as a multiple of the minimum intensity required to elicit the reflex. Electrical stimulation of the dorsal cutaneous branch of the left radial nerve was used. The right elbow joint was fixed at one position throughout the series of recordings (120 degrees). (Decerebrate cat, left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut).

figure it can be seen that if the head or neck is rotated to the left or to the right the reflex threshold decreases or increases respectively. This figure although dealing with reflex threshold on comparison with Fig. 83 (which shows intensity variations in the left triceps) clearly shows that the right extensor muscle receives an abnormal influence from the labyrinth and that the resultant reversal of the conditioning pattern provides inappropriate interaction with neck reflex influences onto that muscle.

3.6.2 The disruption of labyrinth conditioning onto flexor reflex pathways following left hemilabyrinthectomy.

Just as the left extensor muscles show a normal pattern of reflexes in the acute animal so also do the left flexor muscles. This is also true for conditioning influences onto flexion reflexes in left biceps and brachialis observed during rotation of the head (Fig. 89). The effects onto the right flexor muscles are, however, reversed. Head tilts to the left depressing flexion reflexes in the right limb and tilts to the right facilitating these reflexes (Fig. 90). This pattern of modulation in this muscle resembling that observed with neck rotations rather than head tilts in cats with intact labyrinths (see threshold measurements in Fig. 80).

The pattern of neck conditioning influences on extensor reflexes in the acute animal was shown by Figs. 86 and 88 to be normal. Flexion reflex conditioning by changing neck position is also unaffected by left

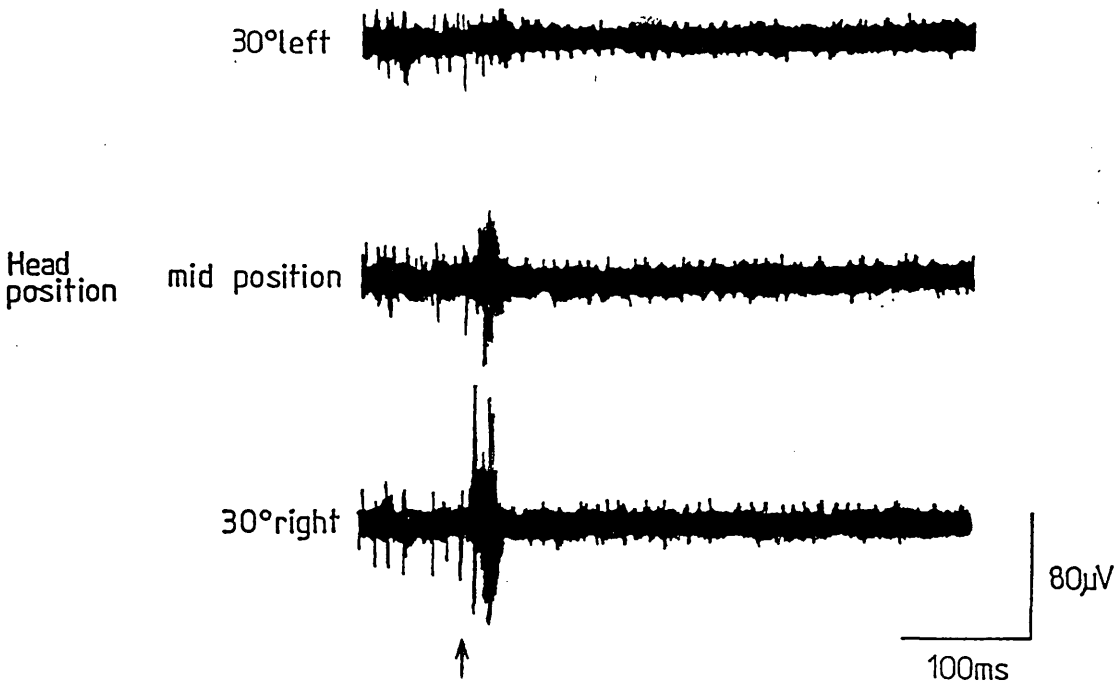


Figure 89. The effect of altering head position on the intensity of the flexion reflex recorded from the left brachialis of an acutely hemilabyrinthectomized cat. Electrical stimulation of the dorsal cutaneous branch of the left radial nerve at a fixed intensity was used throughout. The arrows denote the end of the stimulus train. (Decerebrate cat, left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, axis vertebra clamped).

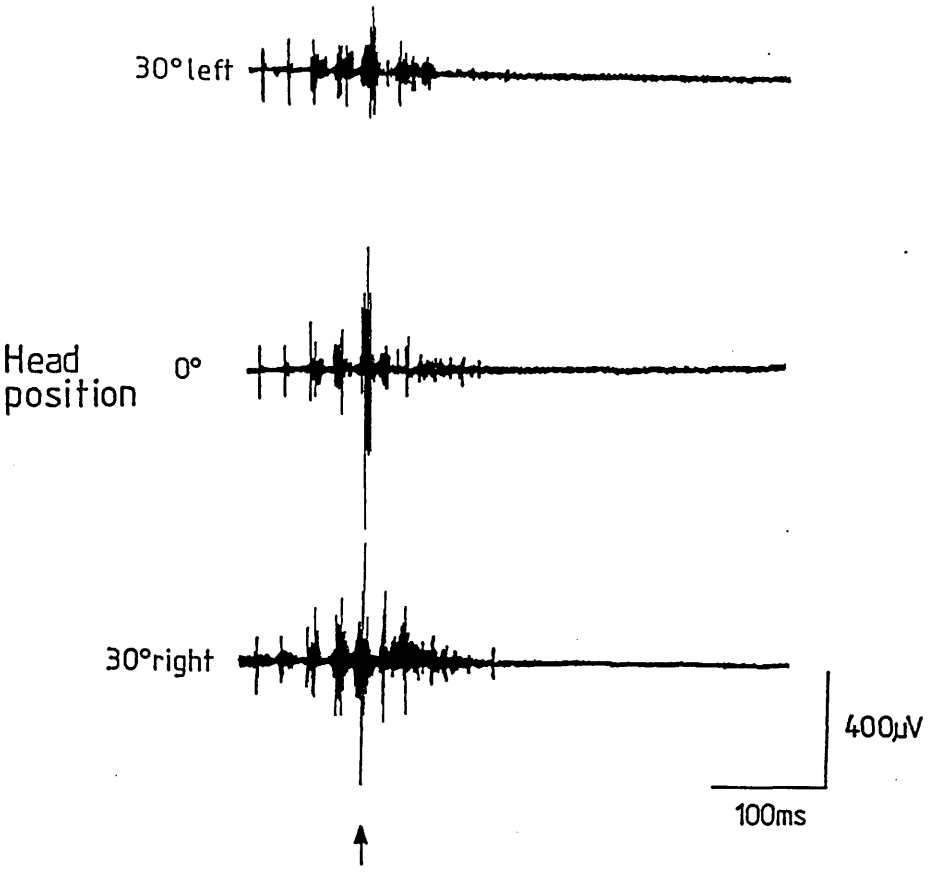


Figure 90. The effect of altering head position on the intensity of the flexion reflex recorded from the right biceps of an acutely hemilabyrinthectomized cat. Electrical stimulation of the dorsal cutaneous branch of the right radial nerve at a fixed intensity was used throughout. The arrows denote the end of the stimulus train. (Decerebrate cat, left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2, axis vertebra clamped).

labyrinthectomy, the magnitude of the reflex in both right and left flexors showing the normal asymmetric (though antagonistic) neck reflex organisation. In addition the positional influence from the limb onto these reflexes is unchanged when compared to normal (Fig. 91). The rectified and integrated EMG's of Fig. 91 showing (right biceps) that the flexion reflex increases in magnitude with side-down neck rotations and the limb held in extended positions. As with the extensors from the right limb, due to the reversal of labyrinth influence following acute hemilabyrinthectomy, the nature of the reflex organisation between head and neck results in synergistic rather than antagonistic reflexes.

The results described above show that descending conditioning influences can alter the expression of crossed extensor and ipsilateral flexion reflexes. Interestingly, in the same experiment as Fig. 91 was obtained from it was noticed that on trying to repeat the same tests that the right biceps now displayed a high level of resting activity, and that presentation of an identical stimulus to the right radial nerve as had been used in Fig. 91 no longer resulted in the normal expression of a flexion reflex. The stimulus resulting in a suppression of EMG activity. However, like the modulation of flexion reflexes in Fig. 91 with changes in neck position the amount of inhibition seen on stimulation was also altered by changing the position of the neck (Fig. 92). Rotations to the left resulted in greater signs of inhibition of spontaneous activity when compared to tests when the neck was in the mid position, while rotations to the right resulted in a

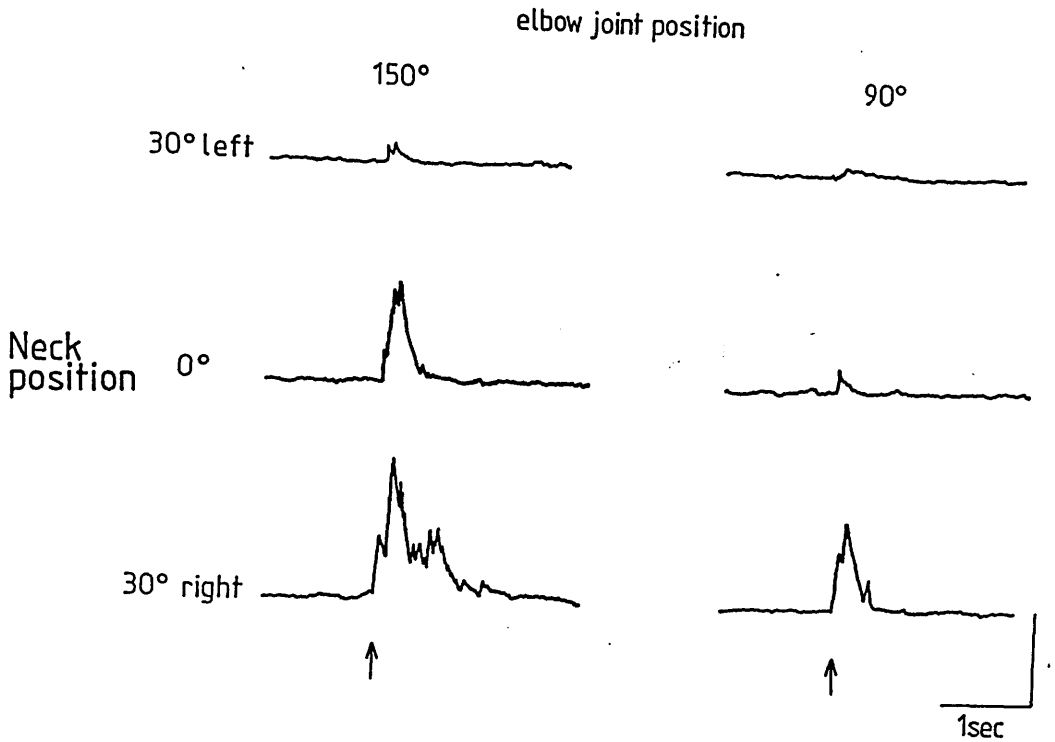


Figure 91. The effect of changing neck and right elbow position on the intensity of flexion reflexes in the right biceps of an acutely hemilabyrinthectomized cat. Electrical stimulation of the dorsal cutaneous branch of the right radial nerve at a fixed intensity was used throughout. The arrows denote the end of the stimulus train. (Decerebrate cat, left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, head fixed in mid-position).

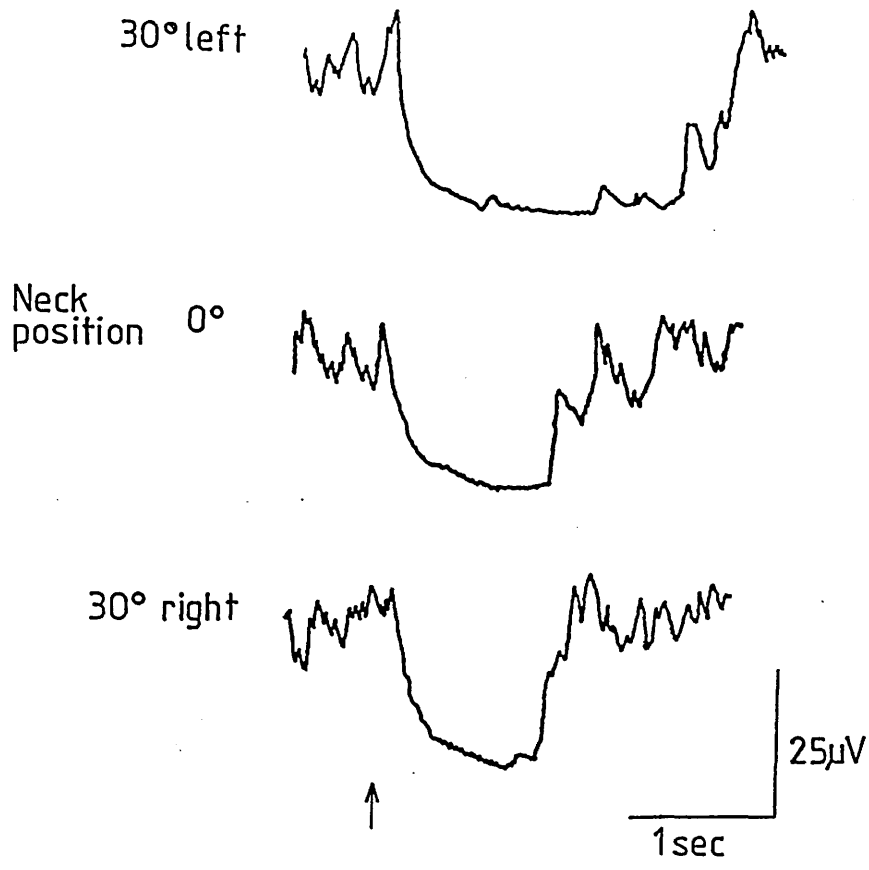


Figure 92. The effect of changing neck position on the abnormal reflex response of the right biceps of an acutely hemilabyrinthectomized cat following electrical stimulation of the right radial nerve at a fixed strength. The preparation and the intensity of stimulation is the same as in Fig 91. The arrows denote the end of the stimulus train. (Decerebrate cat, left hemilabyrinthectomy performed immediately prior to decerebration, C1 & C2 cut, head fixed in mid-position).

reduction in the amount of inhibition evident. Such signs of modulation have direct parallels with those seen when excitatory reflexes result on peripheral stimulation. Neck rotations to the left showing least facilitatory drive and neck rotations to the right revealing the greatest facilitation of the reflex pathways involved. The modulation of what appears as a reversed flexion reflex by changes in neck position reveals that although a variability can be present in the response to peripheral stimulation the descending influences tend to remain acting in one direction.

CHAPTER 4. Discussion.

The results presented in this thesis are discussed in relation to our present understanding of labyrinth and neck reflexes, their interactions and possible functional significance. I will also discuss how the results from acute hemilabyrinthectomized preparations have contributed to our understanding of pathways that may be involved in tonic labyrinth reflexes in normal cats, and finally, how the results gained from chronic hemilabyrinthectomized animals suggest a challenge to contemporary views on compensation from vestibular deficits. The first section of the discussion concerns the adequacy of the natural stimulation techniques in producing labyrinth and neck reflexes.

4.1.0 Adequacy of stimulation.

Cats with intact labyrinths following decerebration have been demonstrated to exhibit reflex reactions in the forelimb musculature to alterations in the position of the head or the axis vertebra. The reactions to positional changes of the head and neck are termed labyrinth and neck reflexes, respectively. In this section of the thesis the adequacy of head and neck tilts in actuating reflexes from labyrinth and neck proprioceptors is argued. The receptor types involved in these reflexes will also be discussed.

In the majority of experiments detailed in this thesis movements of the head and/or the axis vertebra were

used to generate labyrinth and neck reflexes. In order to examine these reflex systems in isolation from each other the technique introduced by Roberts (1963), in which the cervical reflex actions are isolated by sectioning the first two cervical posterior roots, was employed. It is argued that in this preparation with the head, neck and trunk independently supported (as described by Roberts (1963) and later by Lindsay et al., (1976)) and the axes of rotation of the head and neck so aligned as to intersect at the odontoid process of the axis vertebra, that rotations of the head do not result in generating neck reflexes as long as the rotation is restricted to neck regions above C2. Therefore, rotations of the head about a longitudinal axis (following neck denervation) will act as a stimulus to the labyrinths when the axis vertebra is rigidly clamped, while rotations of the axis vertebra should activate receptors below C2.

If one assumes that head tilt following neck denervation, under the conditions described above, does not generate neck reflexes, then what effect will head rotation have on the labyrinths. Head tilts about the longitudinal axis stimulate the labyrinths as a whole, and therefore both semicircular canal and otolith organs will contribute modified afferent inputs to the brain stem. However, as we are dealing with rotations about the long axis, and given that the cat's head is held so that the horizontal semicircular canals lie close to the horizontal plane, then it is possible to exclude these canals from contributing an altered afferent discharge during head rotations. Despite

this, both the superior and posterior semicircular canals can be considered to participate in providing an altered signal to the labyrinth reflex centres. Furthermore, as the adequate stimulus to the semicircular canals is angular acceleration they can only be envisaged to show significant changes in spontaneous afferent activity at the beginning and end of changes in head position.

By considering the acceleration changes experienced by the head and the dynamics of the cupula/endolymph systems, it is possible to gain an impression of how the afferent discharge from the semicircular canals will be affected. The cupula/endolymph system is recognised to behave like a highly damped torsion pendulum (Steinhausen 1931, 1933), which in cats has a long time constant of 3.8 seconds (Blanks, Estes & Markham, 1975). Therefore if an angular acceleration is quickly followed by a deceleration, the deceleration will act on the already displaced cupula tending to restore it to its resting position. Although the adequate stimulus is angular acceleration the cupula displacement and hence afferent discharge, due to the time constants and physical properties of the endolymph/cupula system will reflect the angular velocity experienced by the head. Therefore in a typical head movement, say for example toward the right, the superior and posterior canals of the right side will display a short lasting excitatory burst of activity while the synergist canals of the left side will provide an equally short lasting inhibitory burst of activity, both activity changes will correlate well with the angular velocity of the head. With the reverse

direction of tilt, the responses from the canals are opposite to that stated above. [Inhibition, as used above refers to the effect of the movement of the cupula on the resting discharge of the primary vestibular afferents and not to their central actions of canal afferents.] Therefore the only periods of time during which semicircular canal afferents can contribute to the development of labyrinth reflexes through altered afferent drive are limited to the periods at the begining of a positional change, and at the end of a positional change. Fig. 93 provides an idealised summary of the expected afferent discharge profiles from semicircular canal afferents during a typical positional change. It is evident that this system is incapable of providing a sustained afferent drive with the type of head movement employed in experiments described in this thesis.

Just as we have considered the response of the semicircular canals we can also treat the otolith organs to a similar exercise. These receptors are primarily sensors of linear inertial forces acting on the head, and as such can be envisaged to play an important role in generating the reflexes studied in this thesis. The otoliths are composed of two sensory hair cell beds (1) the utricular macula and (2) the saccular macula. The utricular macula lies in a plane approximately horizontal to the horizontal canal while the sacculus lies close to a parasaggital plane (i.e., orthogonal to the utricle).

Unlike the semicircular canals whose hair cells are uniformly aligned (i.e., have identically directed polarization vectors) the otolith organs show polarization

maps that give a broad directional distribution of polarization vectors. Based on predominant orientation of these polarization vectors it can be seen that utricular neurones should be most sensitive to the lateral tilts originating from an upright head position (see Fernandez & Goldberg, 1976a, b; Goldberg and Fernandez, 1984; and Fernandez et al., 1972). Furthermore, as these neurones are known to show maintained responses to static head tilts and show maximum sensitivity to tilt corresponding with individual polarization vectors (Fernandez and Goldberg, 1976a; Fernandez et al., 1972; Loe et al., 1973; Lowenstein and Roberts, 1950; Vidal et al., 1971), it would therefore seem reasonable to suggest that the greatest afferent response to a lateral head tilt will be seen in utricular afferents. In addition, it has been demonstrated that the majority of otolith neurones show some dependence on tilt velocity in addition to instantaneous head position (Fernandez and Goldberg, 1976a,b). During a head tilt, a typical utricular afferent may show a phasic/tonic response and so contribute to the initial velocity component of the movement as well as to the maintained static head deviation. From a consideration of the semicircular canal and otolith dynamics it can be seen that the utricles will show the greatest sensitivity to the types of head tilt employed in the experiments described in this thesis, but in addition an afferent contribution from the vertical canals may also be apparent during periods of positional change.

From the above considerations it is clear that the

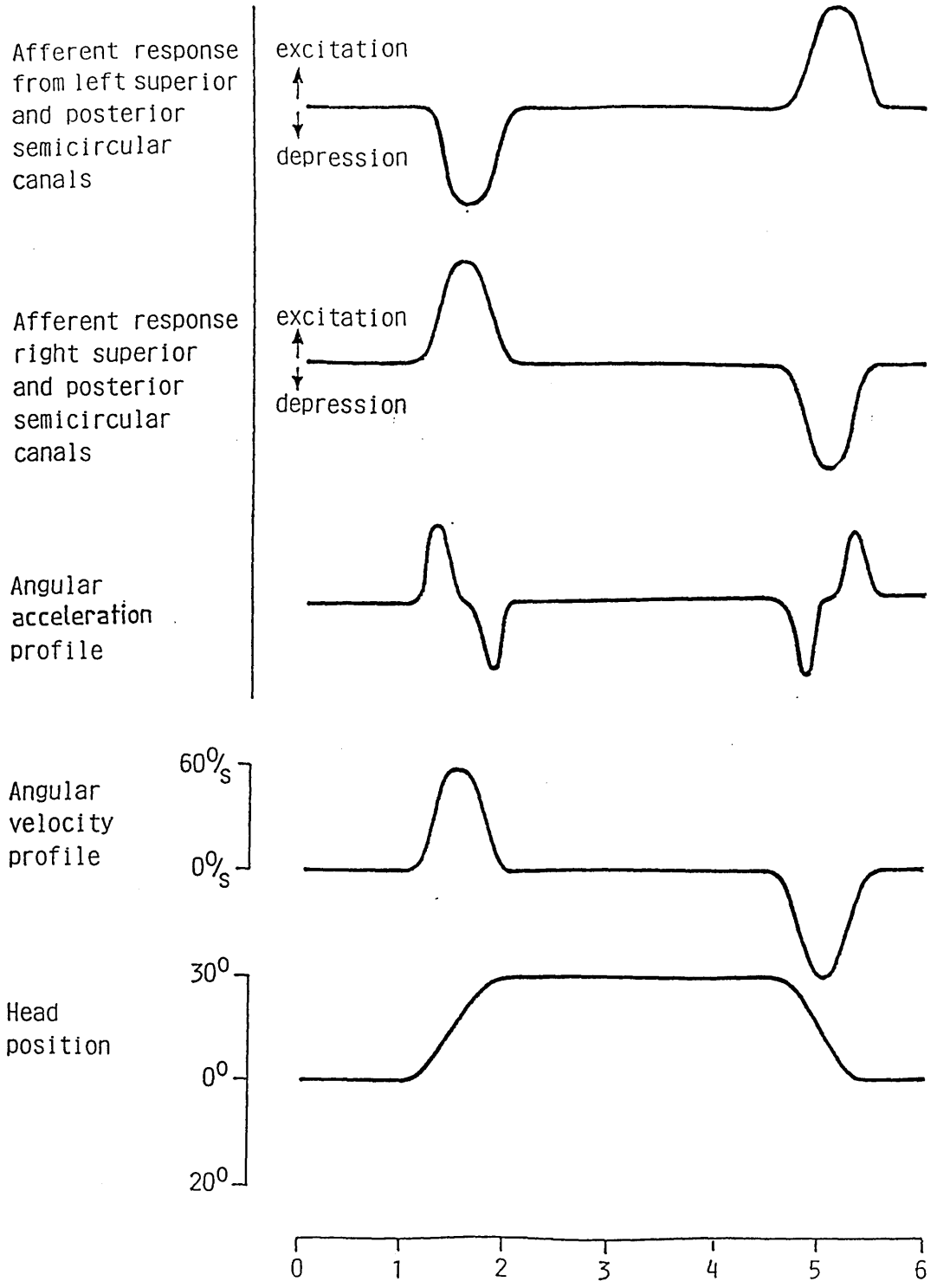


Figure 93. A representation of the angular velocity and accelerations experienced by the posterior and superior vertical semicircular canals and their subsequent afferent discharge during a head tilt.

labyrinths can provide the afferent signals required to elicit tonic reflexes. However, despite the knowledge that a maintained afferent input to the vestibular nuclei can be observed it cannot be concluded (on this basis only) that the tonic reflex results from this maintained discharge.

During a head tilt, in addition to stimulating the labyrinths, it is possible that other receptor systems can be activated that also show a dependance on the duration of the head tilt. Such possiblities may arise as a result of mechanical deformation of the skin or as a result of concomitant muscle stretch.

Rotations of the head are associated to some degree with stretching the skin of the neck. Consequently there may be some contribution from cutaneous receptors to the recorded reflex. Similarly, muscle receptors may also be involved. For example, if during a head movement the scapula moves with repect to the humerus (which is rigidly fixed to the supporting frame), this would then result in stretching the muscles that span the shoulder joint, and may lead to the development of tonic stretch reflexes. Thus, the possibility exists that stretch reflexes may result due to the relative change in position and fixation of elbow and shoulder joints during a rotation of the head. This stretch would last until the head was returned to the normal position, thus any resulting reflex would appear well correlated with the changes in head position. This is also true for any mechanical deformation of the skin.

That these possibilities do not contribute to the recorded reflexes can be argued from the following

considerations. In the majority of experiments the dorsal roots of C1 and C2 are sectioned, thus rendering the skin fields supplied by these roots partially anaesthetic. This 'by product' of the preparation reduces the possible effect that stretching of the skin around the head and neck might have on the results. This on its own, however, is not sufficient to exclude reflex effects from cutaneous receptors, as the skin fields that may be affected by the head rotation lie mainly across the back of the head and overlap with C3 receptive fields, and are therefore not entirely free from innervation. However, manual manipulation of the skin by pulling, to a much greater degree than occurs during head tilts, was never observed to result in alterations of EMG activity when head tilts could easily do so.

That stretch reflexes resulting from rotations of the head due to movements of the scapula may be discounted, since great care was taken to ensure, by appropriate alignment of the head and neck, that the effects of head rotation were confined to areas above the C2 level. In addition close observation both visually and by tactile pressure showed that even during the most vigorous head movements there was no detectable movement of the scapula. Although no movement was observed it can be argued that small movements may have been overlooked. Despite this the involvement of stretch reflexes (and of cutaneous receptor evoked reflex action) can be ruled out if one considers the results of labyrinthectomy. Labyrinth reflexes recorded from cats with intact labyrinths disappear completely

following bilateral labyrinthectomy. In both instances the stimulus (ie the head rotation) is the same, therefore the degree of skin or muscle stretch is comparable in cats with and without labyrinths. It can therefore be argued that involvement of receptor systems outwith the labyrinth would not alter the reflexes recorded on head tilt. That bilateral labyrinthectomy abolishes them is sufficient proof to discount these reflexes as artefacts due to receptor systems other than the labyrinths.

One may then safely assume that reflexes resulting from head rotation are generated from the labyrinth. The next question concerns the possible receptor source for the generation of neck reflexes. These reflexes, as studied in the majority of animals are generated from innervation below C2. In early work on neck reflexes it was independently reported by Sherrington (1910) and Magnus (1926) that these reflexes were lost only after the first three cervical sensory nerves were cut. In an attempt to clarify what receptors from these regions were involved McCouch et al. (1951) carried out experiments designed to test whether the reflex was muscle receptor or joint receptor mediated. By extensively denervating and/or resecting both the muscles connecting the neck and trunk with the occiput, and the intervertebral muscles around the axis and atlas vertebrae neck reflexes could still be seen unmodified following head rotations in labyrinthectomized cats. This observation strongly suggests that muscle receptors are not involved in the reflex. Furthermore by leaving the muscle innervation intact and selectively

denervating the first three cervical joints the response to head rotation was abolished. [The dorsal root ganglia, in the upper parts of the neck, lie proximal to both the dura and the joint ligaments. Careful circumcision of the dorsal root was therefore believed to denervate the joint with little damage to muscular or cutaneous sensory nerves.] With the loss of neck reflexes occurring only after extensive denervation of the neck joints, McCouch et al. (1951) concluded that these reflexes resulted from the activation of receptors in and around the ligaments and capsules of the first three cervical vertebra. However, recent anatomical and histological examination of the receptor content of the tissues surrounding the upper cervical vertebra have questioned the validity of the above conclusion (Richmond and Bakker, 1982; Ferrell, unpublished observation). These studies have consistently found that receptors of the joint regions could not be unambiguously identified as Ruffini endings. The lack of spray endings in these regions is curious, since one might expect from McCouch et al. (1951) results, that neck reflexes would originate from slowly adapting articular mechanoreceptors, however, the lack of such receptors suggests otherwise. Richmond and Bakker (1982) report that the only encapsulated receptors they could find were paciniform corpuscles. These authors also reported that the small complex muscles surrounding the vertebra contain large numbers of muscle spindles and golgi tendon organs. They suggest, in light of the abundance of these receptors, and the apparent paucity of slowly adapting joint receptors,

that proprioceptive information from the tissues around the cervical vertebra originate to a large extent from muscle receptors. This discrepancy between the conclusions of McCouch et al. (1951) may be explained by the sheer complexity of the anatomical architecture of this region of the neck. It is entirely possible that some of the very small muscles and ligaments that span the cervical vertebra were not fully denervated in the way described by McCouch et al. (1951), and that, like the capsular tissues, are innervated by afferents which run back from the proximally located dorsal root ganglia, and are only fully denervated when the dorsal roots are circumcised. The possibility therefore exists that neck reflexes can survive unless these tissues are denervated.

In the surgical preparation of the neck in the experiments reported in this thesis the tissues surrounding the atlanto-occipital and atlanto-axial joints were carefully cleared and the dorsal roots sectioned intradurally. This therefore removes any possibility that either muscle or joint afferents from these regions remain in continuity with the spinal cord, therefore removing the possibility of neck reflexes emanating from this region on head rotation. Although the axis vertebra is cleared to a large extent, to facilitate the fixing of the neck clamp (see 2.1.3 & 2.2.2), the muscular attachments of the interspinous muscles that span the C2-C3 joints are not cleared. Therefore it is entirely possible that the torsion about this joint results in proprioceptors, located within muscle and joints, to be activated and generate neck

reflexes. At present it is impossible to determine what class of receptor participates in this reflex, but it seems likely that muscle receptors play some role in the neck reflex.

The techniques of natural stimulation used in this thesis can be considered adequate for the isolated stimulation of the labyrinths (especially the utricles) and for the activation of neck reflexes via undetermined receptors located in the cervical region.

4.2.0 The normal pattern of labyrinth and neck reflexes seen in decerebrate cats with intact labyrinths.

Lindsay et al. (1976) demonstrated the existence of tonic reflexes in forelimb extensors originating from the labyrinths and neck. This scheme of reflexes challenged existing views on labyrinth and neck reflexes (Magnus, 1926), and provided experimental support for alternative theoretical models of these reflex systems (Lowenstein and Roberts, 1950; von Holst and Mittlestaedt, 1950; and Roberts, 1967 ,1973).

In this scheme of reflexes natural stimulation of the labyrinths, by rotation of the head about a longitudinal axis, was shown to evoke tonic asymmetric reflexes in opposition to those generated by neck reflexes. On the basis of the interaction of these antagonistically organised reflex systems it was suggested, that in the intact animal, the head may be freely moved without altering reflex induced trunk stability. In addition, the

reflex action of the labyrinth and neck on the limbs was thought to compensate for changing forces acting on the trunk during tilting of the support surface. The action on the limbs compensating for changes in the angle of the supporting surface and thereby minimising trunk deviation (Roberts, 1978). The scheme of labyrinth and neck reflexes acting on extensor muscles as described by Lindsay et al. (1976) are confirmed in this study (see section 3.1.2 and 3.1.6) and the reflex organisation and the scheme of reflex interactions extended to include the participation of flexor muscles (see sections 3.1.3 and 3.1.7).

4.2.1 Tonic reflexes in fast muscles.

The tonic nature of the labyrinth and neck reflex in the medial head of triceps is well documented (Lindsay et al., 1976). This muscle is a typical 'postural muscle' with an almost homogeneous population of slow type I muscle fibres (slow oxidative), and is therefore ideally suited for generating sustained fatigue resistant contractions. For a reflex to be described as tonic it has, by definition, to be maintained until the source generating it is removed. Therefore labyrinth and neck reflexes as studied in this thesis can be termed tonic only if they persist, without fatigue, until the position of the head or neck is changed. The definition of a tonic reflex therefore imposes certain requirements on the physiological properties of a particular muscle under study. In view of this, it is not surprising that studies on postural

reflexes have concentrated on the behaviour of the slow red antigravity muscles, which are recognised to be specially adapted for long lasting contractions, much to the neglect of the flexor muscle groups. A situation further exasperated by the tonic state of excitation of these highly oxidative muscles in decerebrate preparations (though see below). Unlike the medial head of triceps, the other heads (the lateral and long heads) are pale muscles with a high proportion of fast fibres. Nevertheless they contain significant numbers of fatigue resistant fibres (type I and type IIa), approximately 43% in both the lateral and long heads. Similarly, the flexors biceps and brachialis, despite being classified as fast muscles contain a large number of fatigue resistant muscle fibres- 49% in brachialis and 41% in biceps (Collatos, Edgerton, Smith & Botterman, 1977). An idea of the relative proportions of the different muscle fibre types in the triceps group and in the flexors biceps and brachialis can be seen from the histochemically stained sections obtained from one cat immediately after death and illustrated in Plates 4 (extensors) and 5 (flexors). Here the significant populations of oxidative (type I) and oxidative/glycolytic (type IIa) fibres can be seen in the different muscles and from this it is evident that these muscles have, though to different extents, the basic machinery necessary for the maintenance of sustained contractions.

Indeed, Denny-Brown (1929) in his extensive investigation of postural reflexes showed that the tonic stretch reflexes occurred in pale as well as red muscles,

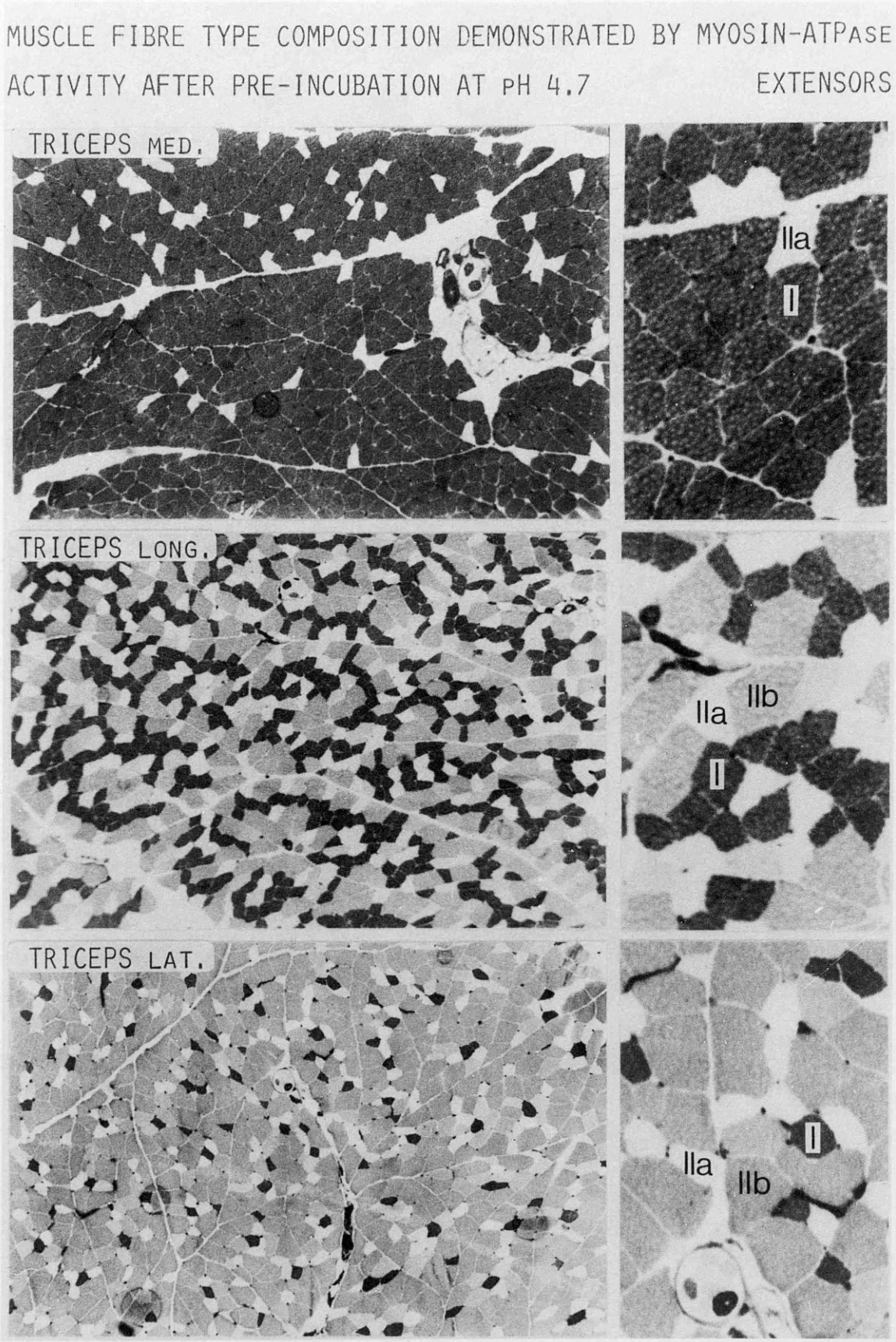


Plate 4. Histochemical profile of forelimb extensors

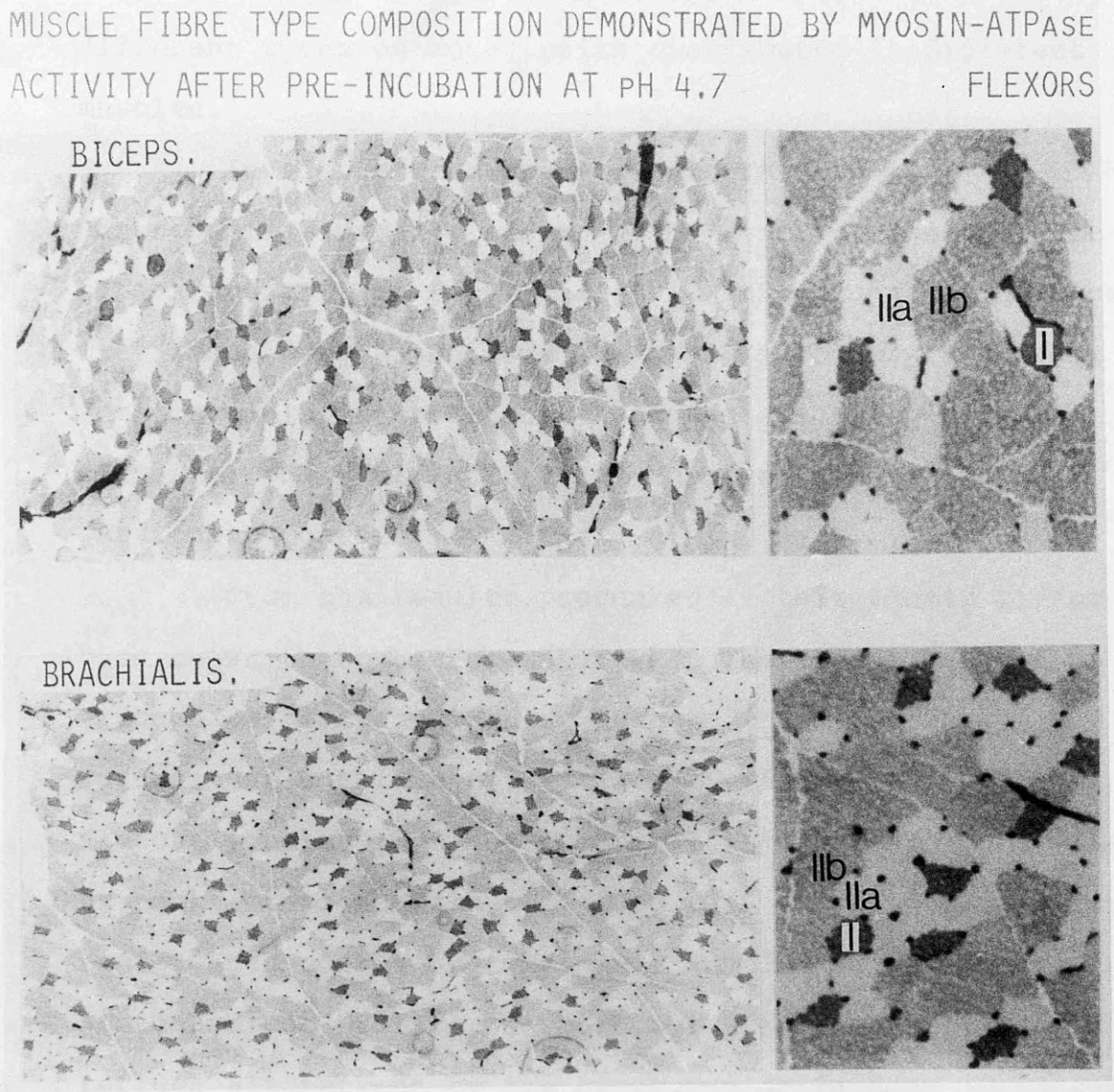


Plate 5. Histochemical profile of forelimb flexors.

although reflex threshold was seen to be lower in the red muscles than in the paler ones. Denny-Brown (1929) suggested that this reflected the threshold of the different types of motor units distributed in different muscles.

In view of the above considerations of histochemical profile and previous descriptions of tonic reflex activity in fast muscles it is reasonable to suggest that these muscles do have the basic machinery necessary for sustaining contractions, and can act along with the classical postural/antigravity muscles in maintaining a particular posture.

From the results presented in this thesis it has been shown that muscles other than the medial head of triceps participate in labyrinth and neck reflexes. Furthermore both the paler heads of triceps and the two flexors studied have been demonstrated to respond to head or neck rotations with responses that can be described as tonic. Such sustained responses, in view of the above histochemical profile of these muscles, almost certainly reflect alterations in the discharge of fatigue resistant muscle fibres. Interestingly, given the mixed composition of these muscles it is possible to speculate not only on which type of muscle fibre is utilized in the tonic component of these reflexes, but also on the genesis of the distinct phasic responses that are also observed.

Just as all three heads of triceps, as well as the flexors biceps and brachialis, commonly exhibited tonic responses, phasic bursts in EMG activity were also

associated with positional changes of the head or neck (e.g. see Figs 7,9,11-14,20,21). The appearance of a phasic component in the EMG can be due to a variety of circumstances. Firstly the positional change itself may provoke an afferent discharge which has a higher dynamic than static sensitivity. A situation which could be expected from the behaviour of semicircular canal and velocity sensitive otolith afferents (see section 4.1.0). Thus the afferent response, during a head tilt would be greatest during the dynamic periods of a positional change when canal and otolith afferents are active simultaneously. This situation could therefore result in greater facilitation of motoneurone pools during such periods and hence provide the synaptic drive responsible for the observable phasic burst of EMG activity. On reaching a static position the contribution from the canals will be lost, and only the tonic response of the otoliths remain.

In a muscle showing a good tonic response to a static head position it may be assumed that the muscle fibres participating are predominately fatigue resistant and are therefore served by small motor neurones. Consequently, in accordance with the size principle (see Burke, 1980; Burke and Rudomin, 1977; Henneman, 1980; Stuart and Enoka, 1983), these units will have a low threshold to afferent input (as first proposed by Denny-Brown (1929)), and therefore can be considered to have been the earliest units recruited by the reflex. However, as described above, the afferent drive responsible for the development of the reflex will be greatest during

the dynamic portion of a head tilt. Thus the synaptic drive during this period may result in these units discharging at a higher rate than that seen during the static phase of the reflex. Similarly the enhanced synaptic drive can be envisaged to recruit not only these small motor neurones but also bring larger motor neurones to threshold. This will then involve the more fatiguable motor units in the reflex, but due to the afferent drive dropping off as the static position is reached the contribution of these units to the reflex will diminish, not only because of lack of a sufficient afferent drive, but also due to their inherent fatiguability. The phasic component of these reflexes may therefore result from the involvement of higher threshold motor units as well as an enhanced rate of low threshold motor units. A similar treatment of neck reflexes can be thought of as involving the utilization of receptors showing dynamic sensitivity as well as those showing position sensitivity.

Although this explanation is theoretically plausible the available evidence supporting this view must be discussed. In the majority of reflexes exhibiting phasic responses, the latter were always associated with the dynamic portion of the stimulus, thereby correlating well with the time that both canal and otolith afferents can be considered as contributing to the reflex. That different motor unit types are recruited during this period is difficult to prove by simple EMG recording. However, studying the nature of typical reflex responses it appears that from multi-unit recordings the phasic bursts are

composed of large amplitude spikes and the tonic reflex component generally of smaller amplitude spikes. If spike size is primarily dependant on the type of motor unit showing activity and not only due to proximity of recording site, then the above considerations can be strengthened in view of the uniformity of the distribution of fibre types within the muscles studied.

However, one must also bear in mind that the tonic component of a reflex may only develop after a considerable latency. Here it would appear that during the time when afferent drive is presumably at is greatest, facilitation is insufficient to bring motor units to threshold, but during the static period, where a diminished afferent drive exists (arising solely from the otoliths), the muscle develops a tonic response (e.g. Fig. 6,26,36) Similarly it was observed that on certain occasions only phasic reflex responses could be recorded. That the phasic component can be observed in isolation in certain situations can be considered compatible with the above view on the source of these reflexes, only if in these instances the units participating are of low threshold, and that during the static component of the test the synaptic drive is incapable of maintaining the firing of these units. In such instances the period of enhanced afferent input during the positional change is sufficient to excite some motor units, but the reduced drive during the static portion is now not capable of maintaining any units above threshold. However, in order to explain why, a tonic component may develop only after a considerable latency (when the presumed synaptic

drive from a positional change has diminished) it is necessary to consider why presumed low threshold units (non fatiguing) may not reach threshold during the dynamic portion of the tilt. One possible explanation for this is that in a specific test the velocity component is small and therefore a large afferent contribution from dynamic receptors can be discounted. Therefore the units recorded may represent the earliest reflex response or may also represent the recruitment of additional motor units during the development of the tonic reflex. If, however, a large velocity afferent signal could be expected, the late reflex may occur because this signal does not interact with the position modulated afferent drive in the expected manner. In terms of the labyrinth reflex this may occur as a consequence of the semicircular canal signal not occurring in synchrony with that from the otoliths. This possibility may result from either different reflex pathways being utilised or from the behaviour of the receptors themselves.

If afferent signals from the semicircular canals reach the limb motoneurones via a different pathway than the otolith signals, then depending on the central state of facilitation in these pathways a situation can be envisaged when transmission via one of these pathways is reduced. Therefore, if transmission via the canal-motor neurone pathway is depressed then the velocity signal may no longer be effective, and threshold will only be reached after the static position has been achieved. A second possibility is that during the tilt, frictional forces in the otoliths

result in the afferent discharge lagging a little behind the movement (i.e., the otolith, despite the change in position, is not displaced immediately -stiction) and so the afferent contributions from the canals and otolith again may be separated, and only the tonic reflex will develop at the longer latency.

In the above treatment of the results obtained from the different forelimb muscles during labyrinth and neck reflexes an attempt has been made to show how various forms of these reflexes can be considered compatible with the physiological properties of the muscles and of the receptors believed to generate these reflexes. In the section to follow the functional relationships between the labyrinth and neck reflex in the different muscles will be discussed.

4.2.2 Reciprocal relationships.

The behaviour of forelimb flexors (biceps and brachialis) during natural stimulation of the labyrinth reveals a strict reciprocal reflex organisation between antagonist muscles in each forelimb. The existence of a reciprocating reflex pattern of labyrinth reflexes is in conflict with previous descriptions of activity changes in antagonist muscles during labyrinthine stimulation (Rademaker, 1935). Rademaker reported that whole body rotations of small amplitude about a fronto-occipital axis were ineffective in augmenting muscular activity, but that displacements greater than 80 degrees from normal induced

marked facilitation in the EMG from both biceps and triceps. This result suggests that coactivation of flexor and extensor occurred on labyrinthine stimulation. From Rademaker's account of these reflexes it is not clear why no sign of altered EMG could be observed until tilts in excess of 80 degrees were encountered, while other studies on labyrinth reflexes (Lindsay et al., 1976; Schor and Miller, 1982; Miller et al., 1982), including the present study, have reported activity changes in forelimb extensors with much smaller tilts. One possible explanation for the differences in results obtained by Rademaker was that in his experiments the cat (decerebrate) was fixed to the tilt table in the lateral position. Although such a set up can allow rotations to be made throughout a complete revolution (something outwith the scope of the present study), any labyrinthine effects could be complicated by reflex actions arising from skin receptors located on the lateral surface of the cat. Possible contamination with afferent input from the skin may occur as a consequence of a weight redistribution over the areas of skin in contact with the tilt table during the excecution of a rotation.

Natural stimulation of the labyrinth has revealed a scheme of forelimb reflexes acting reciprocally between flexor and extensor muscles. A similar response pattern is true following natural stimulation of neck proprioceptors (see Table II). Neck reflexes in this study were observed following rotation of the axis vertebra in cats with partial neck denervation, and by head rotation in a bilaterally labyrinthectomized animal. Despite differences

in the method of inducing the neck reflexes in these preparations no qualitative differences in the form of the reflex could be recognised (see Fig. 24 compared to Fig. 17 & 21). It is important in this respect to note that two different populations of neck proprioceptor give rise to the same reflex pattern. It can therefore be concluded that despite a partial denervation of the neck the innervation remaining from C3 is sufficient to generate neck reflexes that are indistinguishable from those observed in intact neck preparations.

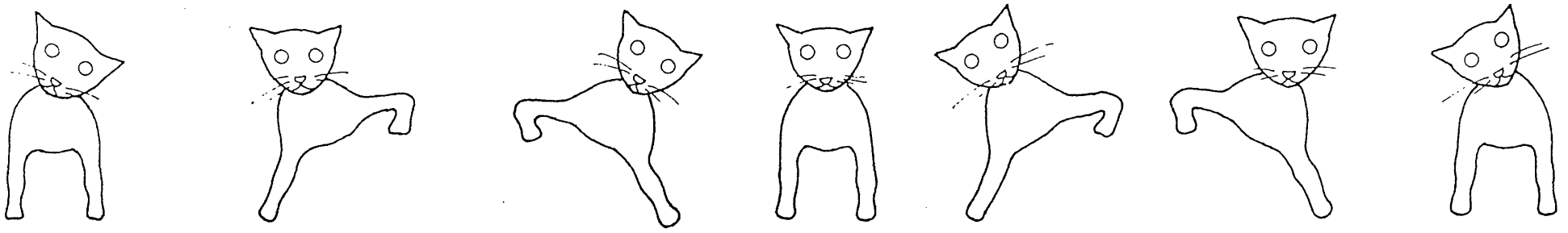
Neck reflexes acting on forelimb extensors show EMG alterations that are consistent with previous descriptions of this reflex (Ezure and Wilson, 1983; Lindsay et al., 1976; Magnus & de Kleijn, 1912; McCouch et al., 1951). The extensor on the side to which the neck is rotated relaxes, while the extensor of the opposite limb actively contracts. Beritoff (1914, 1915) examined the relationship between activity in flexor and extensor muscles in decerebrate cats during various manipulations of the head. Unfortunately, in the majority of his experiments no attempt was made to isolate labyrinth from neck reflexes, and consequently his results are often difficult to interpret. Despite this the experimental protocol adopted by Beritoff suggests on the basis of today's knowledge of labyrinth and neck reflex systems a predominant neck reflex activation, and therefore the existence of reciprocal flexor/extensor neck reflexes. In fact, in one figure from Beritoff's paper (figure 3, 1915) head rotation in a labyrinthless cat is shown to affect activity in the right biceps and triceps brachii in

a reciprocal manner. Thus, in this one example, Beritoff unambiguously demonstrated that the neck reflex influences on flexor muscles are reciprocal to the extensor pattern. Such reciprocal behaviour is confirmed by the present study (see Fig. 24), and, in addition, is recognised as acting antagonistically to labyrinth reflexes resulting from lateral head tilts (compare Fig. 24 to Fig. 15b).

The neck reflex system is organised such that if we consider a quadruped subjected to rotations of the trunk about a longitudinal axis, with the head held stationary in space, then the limb toward which the chin points will extend while the limb towards which the vertex is orientated will actively flex. Similarly, if the whole animal, is tilted about the same axis (the orientation of the head with respect to the neck remaining fixed), then the limb orientation, as governed by the labyrinth reflex, will be asymmetric but opposite to that released by the neck reflexes as described above. This situation is illustrated in Fig. 94 which schematically represents the asymmetry of the labyrinth and neck reflexes, the reciprocal nature of their organisation, and their directional dependance.

Fig. 94, which summarizes the form of the two reflexes in cats with intact labyrinths, also provides a representation of the consequence of the interaction of labyrinth and neck reflexes. As a consequence of the opposing actions of the labyrinth and neck reflexes on an individual muscle, any change in the orientation of the head with respect to the trunk, which also changes the

NORMAL CASE



Head rotated to left. (Interaction of labyrinth and neck reflex)

Body rotated to left (=neck reflex, axis rotated to left)

Body and head rotated to left (=labyrinth reflex)

Normal posture

Body and head rotated to right (=labyrinth reflex)

Body rotated to right (=neck reflex axis rotated to right)

Head rotated to right (Interaction of labyrinth and neck reflex)

Figure 94. Summary of the pattern of labyrinth and neck postural reflexes in the normal cat. The figures illustrate the posture adopted by the animal during independently and simultaneously evoked labyrinth and neck reflexes.

attitude of the neck can result in no apparent change in limb orientation. The form of reflex interaction leaves limb tone unaltered in spite of changes in head and neck position. This scheme was first demonstrated experimentally by Lindsay et al. (1976) and is confirmed in the present study.

4.2.3 Reflex expression is dependent on the level of decerebrate rigidity.

In the decerebrate preparation rigidity is generally considered as an extensor phenomena, although in practice this is not always true (Bazet and Penfield, 1922; Denny-Brown, 1929; Roberts, 1978). The anti-gravity muscles of the limbs show an abnormally high degree of resting tone while the flexors are generally in a more relaxed state. Crossed extensor reflexes are enhanced with regard to excitability while flexor reflexes have a higher threshold than found in the spinal state. Therefore one might expect that reflex systems operating onto flexors as well as extensors would show dependence on the facilitatory and inhibitory mechanisms operating in generating decerebrate rigidity. Indeed, as outlined in the results, variations in the levels of rigidity alter the ease at which manifestations of labyrinth and neck reflexes appear. Labyrinth and neck reflexes onto either extensors or flexors are more readily evoked during periods of moderate rigidity, than in the case of extreme or even absence of rigidity.

The assumed consequence of fluctuating levels of rigidity is illustrated in Fig. 95. In this figure the probability of observing labyrinth or neck reflexes in flexors and extensors is shown to change with altering levels of rigidity. As an animal develops extreme rigidity (either extensor or flexor) it becomes increasingly difficult to observe any labyrinth or neck reflexes. If one muscle group is greatly facilitated the antagonist will be under strong inhibition. Therefore labyrinth and neck reflexes will be ineffective due to saturated activity in one muscle group, while in the antagonists the facilitation from labyrinth or neck reflexes is inadequate in overcoming the inhibition. In a similar way, as the level of rigidity diminishes the muscle group showing greatest activity will show the development of reflexes more easily than the other due to the remaining imbalance in facilitatory and inhibitory influences acting on each muscle group. This suggested explanation for the relation between the fluctuations in rigidity and the appearance of reflexes, can account for the observation that labyrinth reflexes, in the majority of experiments, are most obvious in extensor muscles, since it is these muscles that show greatest background activity. However, on occasions where flexor tone predominates it was seen that not only were the reflexes easier to evoke in the flexors, but in some cases the flexor response was the only event recorded during head or neck tilt.

Despite the influence of fluctuating levels of rigidity during the course of an individual experiment on

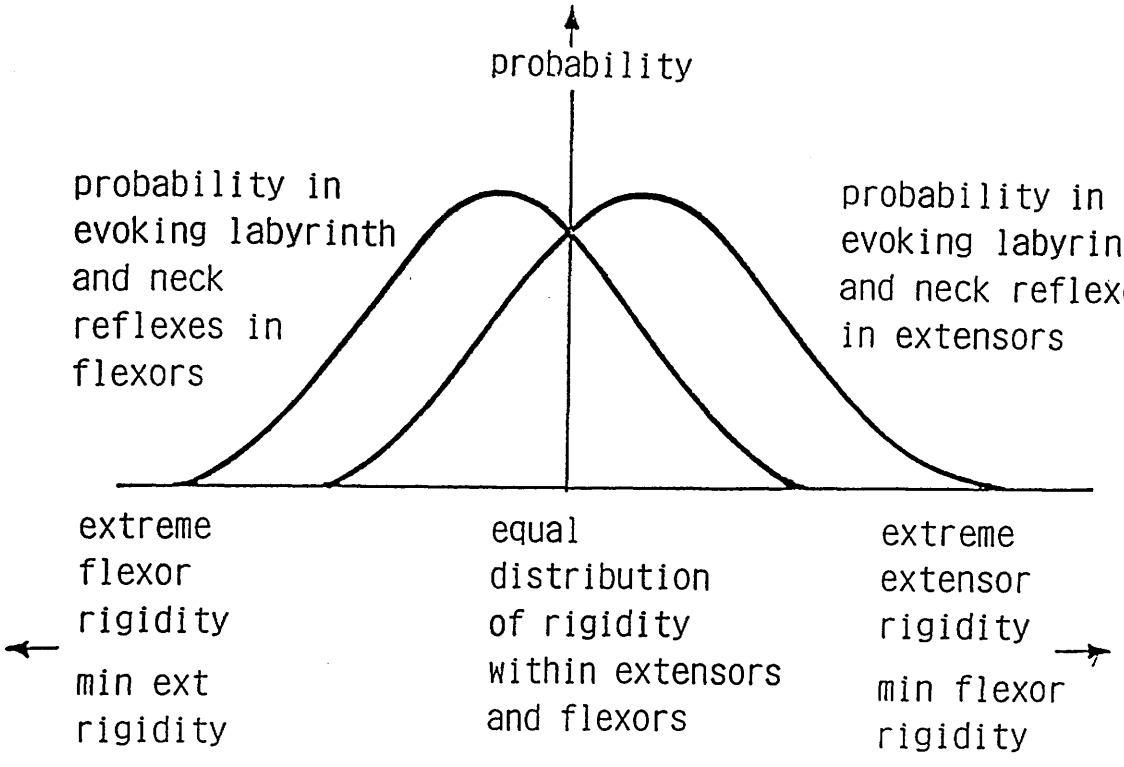


Figure 95. A graphical representation of how changing degrees of rigidity in extensor and flexor muscles alters the ease at which labyrinth and neck reflexes can be observed in these muscles. See text for further information.

labyrinth and neck reflexes, the direction of these reflexes was always constant, with the reflexes being superimposed upon pre-existing levels of background activity. Each head position or neck orientation effectively shifts the bias between extension and flexion in opposite limbs, and thereby altering the rigidity present at any one time in an asymmetric and tonic fashion.

That changes in the symmetry of rigidity occur with alterations in head or neck position suggest the question of whether these reflexes act via pathways common to the generation of existing rigidity or act additively via independent mechanisms. Sherrington (1898) in describing the phenomena of decerebrate rigidity observed that sectioning the appropriate dorsal spinal roots causes a reduction in rigidity, thereby demonstrating the importance of Ia actions onto motoneurones in the maintenance of decerebrate rigidity. However, decerebrate rigidity is not entirely the result of increased activity in the "fusimotor to Ia loop", but is due in part to increased tonic facilitatory drive of supraspinal origin, and in particular to the integrity of the vestibular nuclei. Magnus (1914) reported that an animal was rendered spinal if a section is made caudal to the vestibular nuclei, while Thiele (1905) noticed that division of the vestibulospinal tract in a decerebrate animal resulted in a relaxation of the rigidity on the homolateral side. Similarly Fulton, Liddell and Rioch (1930) and later Bach and Magoun (1947) confirmed that unilateral destruction of the lateral vestibular nuclei (Deiters' nucleus) gives rise to a loss of rigidity

ipsilateral to the lesion, with the rigidity of the contralateral side remaining unchanged or increased. Pollock and Davis (1930b) noted that in anaemic decerebrate preparations deprived of both labyrinths, and with the first four cervical roots cut that rigidity in all limbs was diminished (not abolished) with more or less equal distribution of tone between flexors and extensors. From these observations it has been concluded that the vestibulospinal system provides an important facilitatory influence onto the extensor motoneurones in the development of decerebrate rigidity. It would then seem reasonable to suggest that the labyrinths act via centres partially responsible for decerebrate rigidity, since the vestibular nuclei represent the site of termination of the majority of primary vestibular afferents, and are known to influence the behaviour of neurones in these nuclei. Also, it is known that the lateral vestibulospinal tract takes its origin in the lateral vestibular nucleus, which is the main site for the projection of otolith afferents believed to be responsible for tonic reflexes (Brodal et al., 1962), and is also a site for convergence of neck and labyrinthine signals (Boyle and Pompeiano, 1981). Therefore, since decerebrate rigidity is partially dependant on the activity of cells that project to the cord from the lateral nucleus, any system which alters the activity of these cells can also influence the amount of rigidity present at any one time. An obvious example of this is evident following hemilabyrinthectomy. The loss of one labyrinth results in a reduction in the tonic activity of vestibular nuclear cells

ipsilateral to the lesion and an increase in the activity of cells from the intact side (Precht, 1974; Xerri, Gianni, Manzoni and Pompeiano, 1983). This asymmetry in resting activity in the vestibular nuclei suggests a mechanism for the asymmetric decerebrate rigidity which develops following unilateral labyrinthectomy. Similarly, in chronic hemilabyrinthectomized animals following the re-establishment of activity in the vestibular nuclei ipsilateral to the lesion no hypotonia is evident following decerebration. It would therefore appear that the labyrinths, and to some extent the neck proprioceptive afferents, by being able to influence the behaviour of vestibular nuclear cells can influence centres involved in generating ipsilateral rigidity. This, however, does not necessarily mean that the labyrinth reflexes are expressed through this mechanism, as will be made clear when the results from acute hemilabyrinthectomized animals are discussed.

4.3.0 The pattern of labyrinth and neck reflexes seen immediately following unilateral labyrinthectomy.

The above sections have discussed the normal pattern of labyrinth and neck reflexes observed in forelimb extensors and flexors. In this section the alteration to this pattern following left hemilabyrinthectomy will be discussed.

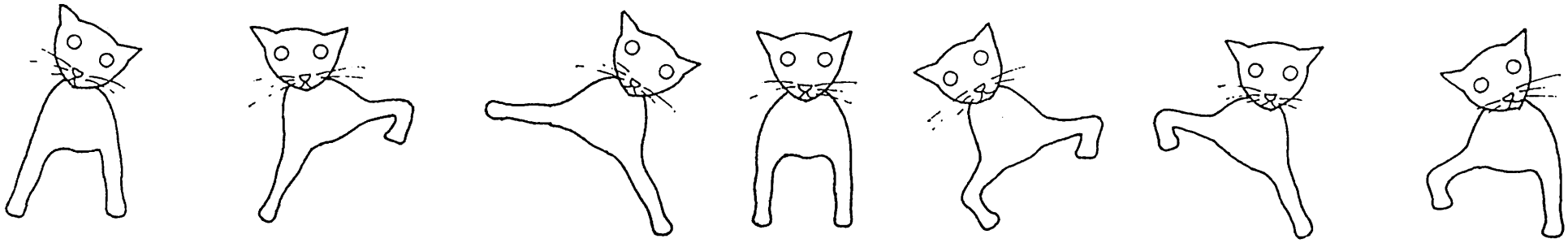
In animals with intact labyrinths reflexes arising from lateral head tilts are asymmetrically organised.

Following hemilabyrinthectomy this asymmetry is lost and the tonic labyrinth reflex becomes symmetrical (see Figs. 26, 28 & 36). The tonic reflex acting on forelimb extensors is reversed in the limb contralateral to the lesion, whereas the reflex ipsilateral to the lesion remains normal. This result was first shown by Nagaki (1967) and later by Lindsay and Rosenberg (1978). This finding is confirmed in this study, where following destruction of the left labyrinth the left triceps is seen to behave in a normal manner following head tilt, while the right triceps shows a reversal in behaviour. In addition to the alteration in the extensor pattern of labyrinth reflexes the activity of the flexor musculature is also altered following hemilabyrinthectomy. The alteration in the behaviour of the flexor muscles in the majority of animals studied parallels the changed extensor reflex such that a reciprocal organisation between antagonist muscles in one limb remains despite the loss of the left labyrinth (see Figs. 31, 32, & 33). Thus head tilts reveal a reversal of both the extensor and flexor labyrinth reflex in the right forelimb. In consequence head rotation toward the lesion (left side) results in augmented extensor activity in the left and right forelimbs with simultaneous flexor relaxation, while tilts toward the side of the intact labyrinth result in left and right flexor coactivation with a synchronous depression of extensor activity (see Table III).

The neck reflex, as revealed in acute hemilabyrinthectomized animals by rotation of the axis

vertebra, shows no apparent differences to those observed to occur in the normal group of animals. These reflexes retain their asymmetric organisation. Consequently, the labyrinth and neck reflex in the acute animal no longer act in direct opposition to each other as in normal animals. The situation is summarised in Fig. 96 which schematically sets out the labyrinth and neck reflex in the acute hemilabyrinthectomized preparation. The figures which depict these reflexes try to illustrate the direction of activity change associated with labyrinth or neck stimulation, but do not take into account pre-existing tone within the limbs. Fig. 96 compared with Fig. 94 illustrates the labyrinth and neck reflex in the normal cat and the consequences of the disruption to the reflex organisation following unilateral labyrinthectomy. In the intact animal head movements actuating both labyrinth and neck reflexes result in the mutually antagonistic reflexes summing to zero, while in the acute animal such a head movement due to the abnormal labyrinth reflex in the right limb no longer results in opposing reflexes (Figs. 48 & 49). The reversed labyrinth reflex in the right limb now acts in the same direction as neck reflexes to produce extensor facilitation with head tilts to the left and increased flexor activity with tilts to the right in this limb. In the normal animal the interaction of labyrinth and neck reflexes can provide a reflex system suitable for the maintenance of postural stability during head movements, whereas the reflex organisation in the acute hemilabyrinthectomized preparation can no longer support such a scheme. The

ACUTE LEFT HEMI-LABYRINTHECTOMY (uncompensated)



Head rotated to left. (Interaction of labyrinth and neck reflex)

Body rotated to left (=neck reflex, axis rotated to left)

Body and head rotated to left (=labyrinth reflex)

Normal posture

Body and head rotated to right (=labyrinth reflex)

Body rotated to right (=neck reflex axis rotated to right)

Head rotated to right (Interaction of labyringth and neck reflex)

Figure 96. Summary of the pattern of labyrinth and neck postural reflexes in cats in which the left labyrinth has been destroyed (acute preparations). This figure in comparison with Fig 94 highlights the reversed labyrinth reflexes in the right limb and the subsequent abnormal labyrinth and neck reflex interactions in these animals.

interaction of the labyrinth and neck reflex leads to the development of an unstable posture.

Unilateral labyrinth destruction results in a rotation of the head toward the lesion, exaggerated extensor tonus on the intact side and hypotonus on the side of the lesion. These postural disturbances seen in acute animals were stated by Magnus (1926, see also Camis, 1930) to result from labyrinth reflexes acting on the head (leading to head rotation), which in turn generates neck reflexes which act to produce the aysmmetric limb attitudes. The limb toward which the chin points (contralateral to the lesion) exhibits an increased extensor activity while the opposite limb (ipsilateral to lesion) shows diminished extensor tone. The postural deficits of the animal were therefore believed to result as a secondary consequence of the labyrinthectomy, namely, the expression of neck reflexes resulting from the head rotation. That such a scheme cannot account fully for the observed postural deficts can be judged by the maintenance of the asymmetry in limb attitude when, in the decerebrate animal, both the head and neck are held in the normal position. The loss of tone ipsilateral to the lesion is a deficiency symptom resulting from the labyrinthectomy to which the postural consequences of head attitude with respect to body position, and the abnormal form of labyrinth reflexes must be added.

On the basis of the results from experiments describing the pattern of labyrinth and neck reflexes in acute hemilabyrinthectomized animals a mechanism accounting

for the observed postural abnormalities can be proposed.

The asymmetric distribution of tone between left and right limbs is a result of a deficiency in ipsilateral extensor facilitation following the loss of one labyrinth. The hemilabyrinthectomy causes a reduction in the activity of vestibulo-spinal tract neurones (Xerri et al.,1983). In addition, there is a disruption of the vestibular control over the neck muscles such that the head becomes rotated toward the lesion. As a consequence both labyrinth and neck reflexes will be generated. Consider the consequences of a left labyrinthectomy. The limb ipsilateral to the lesion shows normal interactions between labyrinth and neck reflexes. The existing distribution of tone in that limb will therefore not change during movements of the head upon the neck. However, in the limb contralateral to the lesion the labyrinth reflex is abnormal, and therefore the form of the interaction with the neck reflex is altered. For example, head rotation to the left (side of lesion) will result in labyrinth and neck reflexes both acting to increase the extensor tone in the right limb. The extensor tone on the intact side following head rotation to the left is therefore augmented by the abnormal interaction of labyrinth and neck reflexes, while the tone on the side of the lesion remains unchanged by labyrinth and neck reflex interaction, although it is diminished as a secondary consequence of the loss of facilitation from vestibulospinal systems following the labyrinthectomy.

The above argument suggests that the abnormal interaction of labyrinth and neck reflexes on the side of

the remaining labyrinth can account for the exaggerated extensor tone on that side. The consequences of this abnormal interaction between labyrinth and neck reflexes may also account for some other observations made on behaving cats during acute stages of recovery. Cats following unilateral labyrinthectomy are consistently observed to be unable to maintain a stable position during voluntary head movements. An animal attempting to move its head is thrown onto its side, with falls toward the side of lesion occurring most commonly. The tendency to fall is a result of the abnormal reflex interaction acting on the limb contralateral to the lesion. The drawings of Fig. 96 which illustrate this interaction reveal that a head rotation to the left increases right extensor activity, which coupled with the diminished extensor tone on the side of the lesion will effectively throw the animal toward that side. If the animal makes a head movement to the right, the right limb is thrown into flexion and the animal once again becomes unstable and will fall. It can be seen, therefore, that some of the postural abnormalities observed in the acute preparation are not solely deficiencies resulting from the loss of the labyrinth, but are the result of a reversal in the labyrinth reflex on the intact side producing interactions with neck reflexes that are no longer appropriate for postural stability.

The observation that the labyrinth reflex ipsilateral to the lesion appears normal, while that contralateral becomes reversed poses the question of what pathways are responsible for these reflexes in the normal

cat. This topic will be dealt with in the following section.

4.3.1 Labyrinth positional reflexes are mediated by a contralateral pathway.

The vestibular nuclear complex can influence the spinal cord by two spinal tracts, the medial vestibulospinal tract and the lateral vestibulospinal tract (see review of the vestibular system by Goldberg and Fernandez, 1984). However, only the lateral vestibulospinal tract has been demonstrated to influence limb musculature (see review by Wilson and Peterson, 1978), whereas the medial tract acts mainly on neck and axial musculature (Wilson et al., 1970).

The lateral vestibulospinal tract arises from cells located in Deiter's nucleus and projects ipsilaterally to all levels of the spinal cord (Brodal, 1974). This tract is believed to convey macular information to the spinal cord as it arises from regions with a high density of primary otolith afferent terminations (Brodal et al.,1962). Indeed, tilt sensitive secondary lateral vestibulospinal projecting cells have been found in studies utilising natural labyrinthine stimulation (Boyle and Pompeiano, 1980; Peterson, 1970; Schor, 1974). These cells have monosynaptic excitatory effects on some hindlimb extensors (Lund and Pompeiano, 1968; Wilson and Yoshida, 1969) and inhibitory actions mediated by Ia inhibitory interneurones to flexor motoneurones (Grillner, Hongo & Lund, 1966). No

monosynaptic projection to forelimb extensor motoneurones exist, but excitatory potentials are recorded bilateraly with disynaptic latency following electrical stimulation of Deiters' nucleus, and a trisynaptic latency on direct electrical stimulation of the vestibular apparatus (Wilson and Yoshida, 1969; Maeda et al., 1975). Forelimb flexors are mainly inhibited following electrical stimulation of the labyrinth. Latency measurements suggest a pathway involving four synapses (Maeda et al., 1975). From such studies, and from the obvious loss of extensor facilitation seen on lesions to the lateral vestibulospinal tract, Deiters' nucleus has been considered an important relay from the labyrinth to the limb musculature, and therefore could play an important role in the generation of tonic labyrinth reflexes.

To what extent, given the ipsilateral termination of the vestibulo-spinal tract onto extensor motoneurones, can the pattern of normal labyrinth reflexes be explained by the action of this pathway? In an attempt to answer this question, the action of head tilt on extensor muscles shall be considered, the involvement of the flexors shall be considered later.

The operation of an ipsilateral labyrinth reflex, i.e., one dependant on the ipsilateral lateral vestibulospinal tract, as revealed by head tilt must have the following property: to allow increases in ipsilateral extensor activity with side-down head tilts it is necessary that utricular units excited by side-down tilt mediate the reflex. The situation detailed in Fig. 97 could then

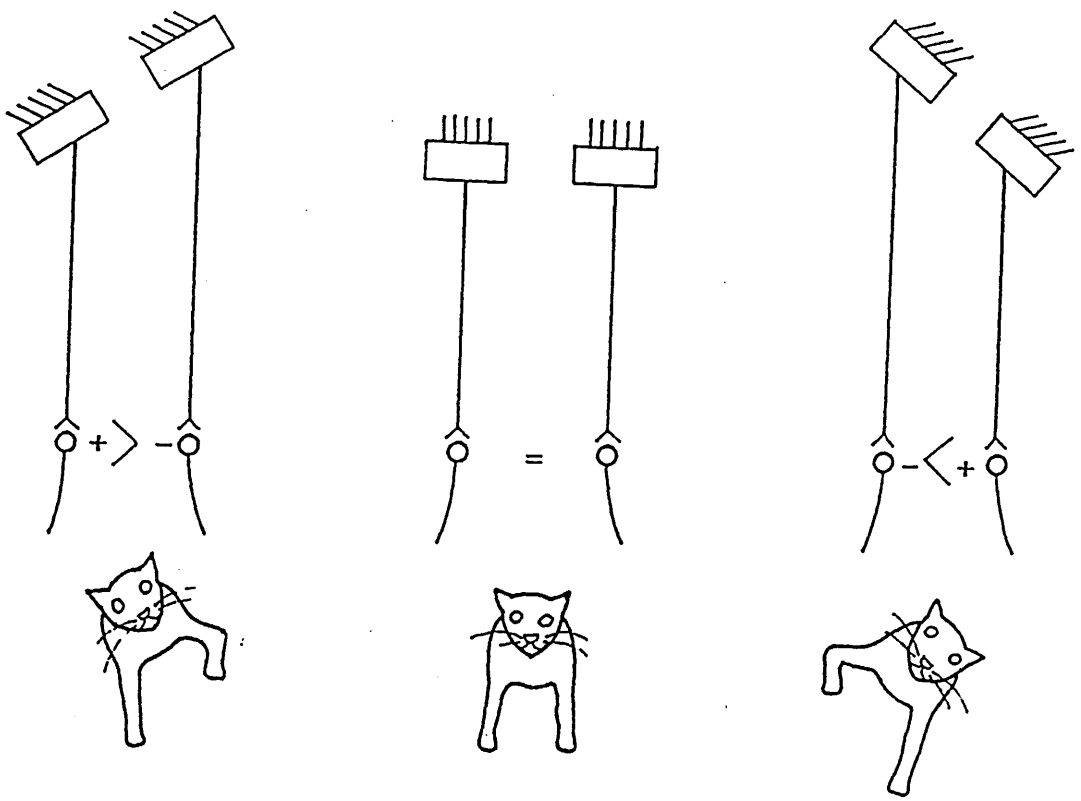


Figure 97. Hypothetical ipsilateral facilitation of extensor motoneurones from the otoliths. In order to provide the normal pattern of asymmetric labyrinth reflexes in extensor motoneurones the above pathway requires utricular afferents, mediating the reflex, to increase their discharge with side-down tilts and decrease their output with side-up tilts.

operate. In this figure the effect of tilt on the otoliths from opposite sides result in an asymmetry in utricular afferent discharge which results in asymmetric reflexes in opposite extensors. This result is consistent with the existence of an ipsilateral pathway from labyrinth to extensor muscle utilizing the lateral vestibulospinal tract. If one assumes this pathway as a model for labyrinth reflexes, then unilateral labyrinthectomy will result in predictable alterations to the labyrinth reflex. Therefore, assuming an ipsilateral reflex operates, then the consequences of a unilateral labyrinthectomy are as follows. The reflex on the side of the lesion will be lost following hemilabyrinthectomy and that on the intact side will remain normal. This situation is illustrated in Fig. 98. However, as previously described the experimental results obtained from animals subjected to unilateral labyrinthectomy do not conform to this model (Figs. 26 to 39).

In the acute animal the labyrinth reflex on the side of the lesion is normal while that on the side of the intact labyrinth is reversed. The experimental results, therefore suggest that an alternative pathway to that illustrated in Figs. 97 and 98 must operate. It is proposed that a pathway similar to that shown in Fig. 99 operates in the acute hemilabyrinthectomized cat. Since head tilt in an acute preparation can only influence the limb musculature by activity emanating from the remaining labyrinth, and that left and right limbs show symmetrical labyrinth reflexes, then it is necessary that a crossed pathway, in

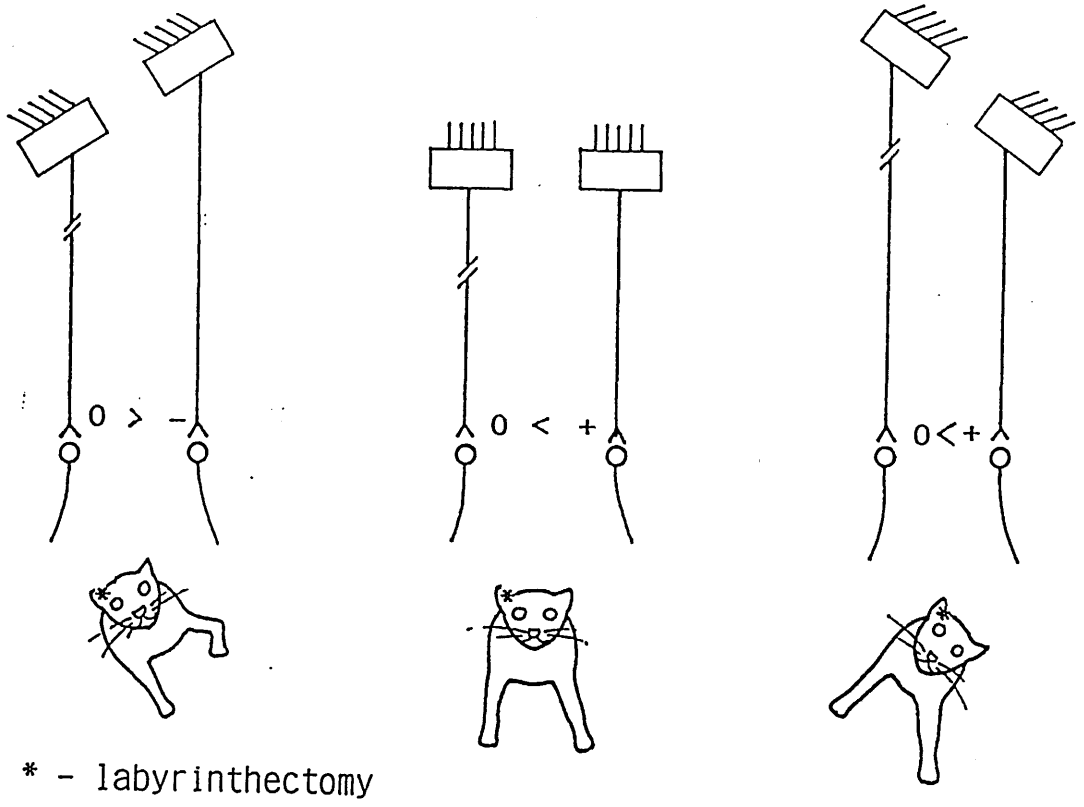


Figure 98. Predicted outcome upon the labyrinth reflex following hemilabyrinthectomy if the scheme of Fig 97 operates. With an ipsilateral pathway mediating otolith reflexes, hemilabyrinthectomy would only affect reflexes on the side of the lesion. The pattern of reflexes on the unoperated side should appear normal.

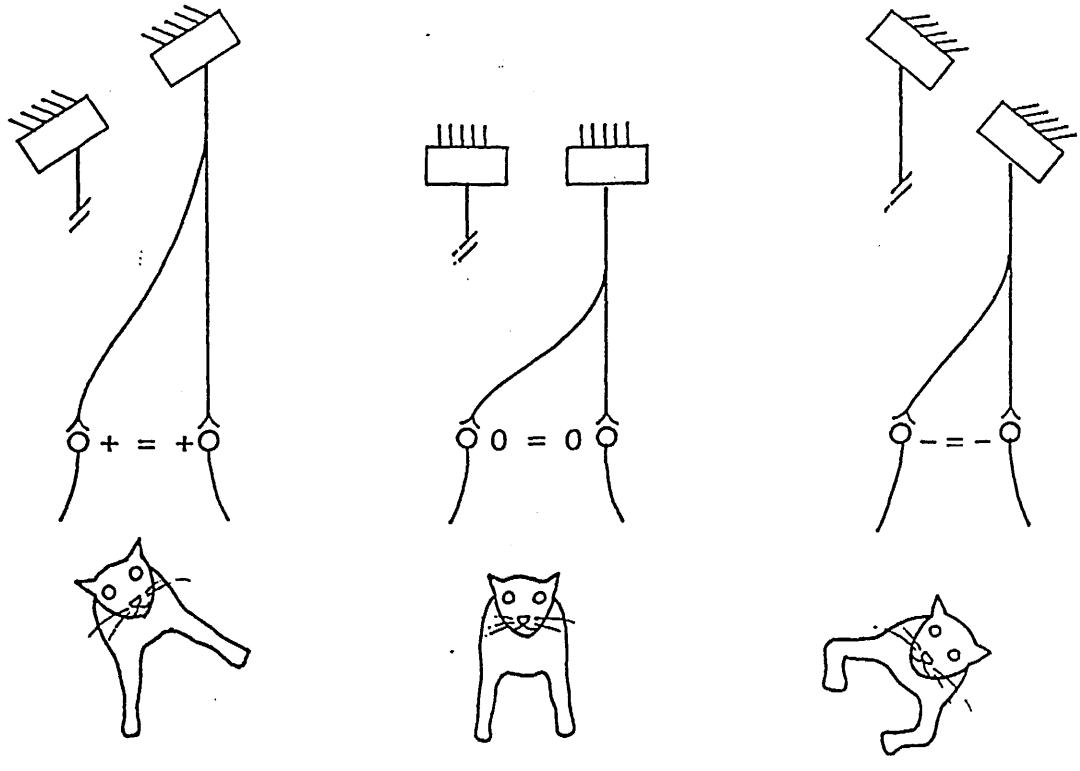


Figure 99. Proposed pathway from the otolith to extensor motoneurones that can explain the experimental observations on the labyrinth reflex in hemilabyrinthectomized cats. Unilateral labyrinthectomy results in symmetrical reflexes in forelimb muscles following head tilt. The reflexes on the operated side being normal and those on the intact labyrinth being reversed. This can be explained by the presence of both a crossed and uncrossed pathway to extensors which are mediated via utricular afferents that increase discharge with side-up tilts.

addition to an ipsilateral projection must exist. Furthermore, as the form of the reflex is symmetrical between left and right sides the contralateral and ipsilateral pathways act with the same sign. An important point is that the labyrinth reflex is normal on the side of the lesion, which suggests that utricular units excited by side-up tilts mediate the reflex, which may also explain why the reflex contralateral to the lesion is reversed. From such considerations concerning the disruption of labyrinth reflexes in the acute animal it appears that utricular afferents showing an increase in discharge during side-up tilts can provide the central nervous system with the necessary afferent input required for the generation of otolith reflexes without the need for extensive central modification. Supportive evidence for this comes from a study in which the dynamic response of secondary vestibular neurones projecting to the spinal cord were compared with the dynamic characteristics of the labyrinth reflex in forelimb extensors in canal plugged cats (Schor and Miller, 1982). This study revealed a strong correlation between the behaviour of beta cells (increase discharge side-up) and the phase characteristics of contralateral forelimb extensors.

The results from hemilabyrinthectomized animals suggest that the scheme portrayed in Fig. 97 cannot operate in cats with two functioning labyrinths. The situation in the normal cat has to function as illustrated in Fig. 100, where both labyrinths act via ipsilateral and contralateral pathways. In view of this, and bearing in mind that the

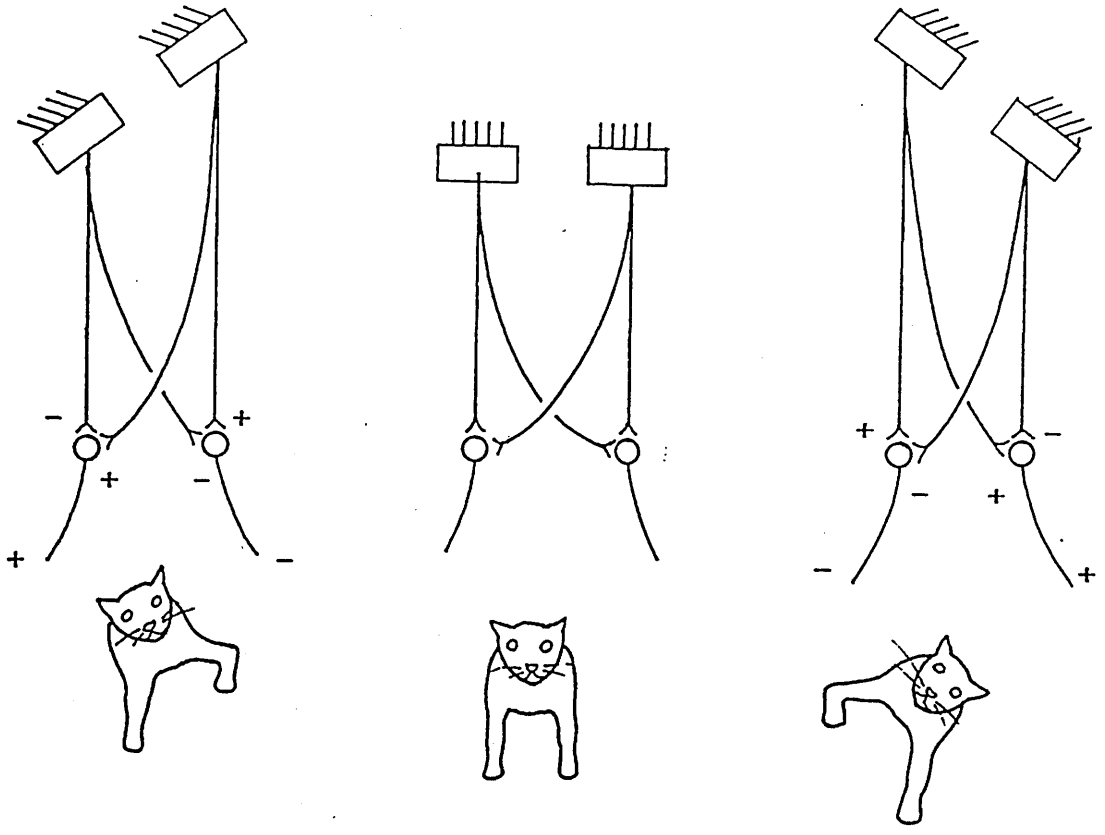


Figure 100. Proposed scheme in the intact animal that allows the expression of the normal asymmetric labyrinth reflex. In the intact animal the crossed and ipsilateral pathways, as proposed from the results from hemilabyrinthectomized cats (see Fig 99), will converge on extensor motoneurones, therefore, in the generation of the normal labyrinth reflex the crossed pathways must dominate over the ipsilateral otolith-extensor motoneuronal pathways.

bilateral projection from one labyrinth is mutually antagonistic to that from the opposite labyrinth, it is necessary for the contralateral projection from each labyrinth to dominate in order to provide asymmetric labyrinth reflexes.

Similar conclusions follow from experiments carried out on animals subjected to spinal lesions. Miller et al. (1982) studied the effects of vestibulospinal lesions on roll-tilt reflexes. The result of this study demonstrated that medial vestibulospinal tract lesions (section to the medial longitudinal fasiculus) do not have a major effect on labyrinth reflexes, but that hemisection of the cord invovling the lateral vestibulospinal tract, (lesions to reticulospinal tracts also be noted to have occurred) induced two major effects on the extensor behaviour of the forelimb. The lesion altered the reflex behaviour of the extensor contralateral to the lesion by inducing a phase reversal in the reflex response of the muscle. In addition, the classical result of a loss of extensor activity ipsilaterally on lateral vestibulospinal tract lesion was observed, with a partial loss of rigidity on the intact side. The phase reversal contralateral to the lesion and the normal form of the reflex ipsilateral to the lesion support the idea that the tonic labyrinth reflex is predominately mediated by contralateral pathways.

Miller et al.'s (1982) observation of a loss of extensor tone contralateral to the lesion is opposite to the result seen following hemilabyrinthectomy, where extensor tone is heightened rather than reduced. An

explanation for this difference in extensor tone in the different preparations is outlined below. In Miller et al. (1982) the lesions were carried out at C2-C3 levels which leave the activity of cells within the vestibular nuclei largely unaffected, whereas hemilabyrinthectomy suppresses the tonic activity of these cells ipsilaterally, and may facilitate cells of the opposite lateral nucleus due to the removal of cerebellar inhibition (see discussion Xerri et al., 1983). Therefore no hypertonia contralateral to the lesion is seen in the experiments of Miller et al. (1982) as facilitation from the intact vestibulospinal tract is not altered (as occurs with hemilabyrinthectomy). The observation that a hypotonia develops in the contralateral limb following section of the ipsilateral vestibulospinal tract can be explained by the removal of the postulated contralateral facilitatory pathway.

From the results of hemilabyrinthectomy it is difficult to be certain if the major contralateral pathway from labyrinth to extensor is crossed at the level of the brain stem or the spinal cord. The observation of tilt sensitive neurones in the lateral vestibular nucleus following desruction of the labyrinth illustrate that a projection from the intact side to the deafferented side exists, thereby indicating the possibility of a crossed brain stem pathway (Xerri et al.,1983). However, the observation that spinal hemisection results in a phase reversal on the intact side (Miller et al., 1982) indicates the presence of a major pathway from labyrinth to contralateral extensor crossing within the spinal cord.

Labyrinth reflexes can be recognised to act mainly via contralateral pathways mediated by secondary vestibular neurones that increase their discharge with side-up tilts. In Fig. 100 the contralateral and ipsilateral projections are illustrated for cats with two functioning labyrinths. However, in addition to the ipsilateral pathway illustrated in Fig. 100 (showing decreased activity with side-down tilts) an ipsilateral projection from cells exhibiting increased activity with side-down tilts (as described for Fig. 97) can be envisaged. Two actions may therefore accompany the ipsilateral projection from the otloliths to the extensor motoneurone pools. One action resulting from the beta cell mediated effect, as postulated from the results of hemilabyrinthectomy, and the other from an hypothetical alpha cell generated effect. Assuming that these actions are not altered by neural filtering, a lateral tilt of the head will result ipsilaterally in opposing actions from the two types of lateral vestibular nuclear cell. This implies a heirarchy of effectiveness onto motoneurones in the generation of static labyrinthine reflexes. In the absence of the dominant contralateral input, as occurs following hemilabyrinthectomy or spinal section, the opposing ipsilateral actions on the intact side are resolved in the favour of beta actions.

To provide a normal asymmetric reflex on head tilt the contralateral pathway is seen or is suggested, from the experimental results of this study, to be more important than the ipsilaleral pathways. Of the ipsilateral actions the next most effective pathway to the contralateral one is

the ipsilateral beta mediated action, which in turn dominates over the ipsilateral alpha mediated input. An extensor motoneurone can be considered to receive three inputs (1) contralateral beta, (2) ipsilateral beta and (3) ipsilateral alpha. The alpha action when in the presence of the contralateral beta input may assist in offsetting the opposing actions from the ipsilateral beta projection to provide appropriate input for the generation of the labyrinth reflex.

Results from experiments ulilizing electrical stimulation of the labyrinth provide additional support for the above scheme. Forelimb extensor muscles receive synaptic input from both ipsi- and contralateral labyrinths (Maeda et al., 1975). Unlike natural stimulation of the labyrinth, where one population of vestibular afferents may respond with an increase in activity and another a decrease, electrical stimulation results in a non-specific increase in all afferents. The results of such studies therefore indicate what pathways are available, but do not provide any information on the functional significance of these pathways. Despite this, certain parallels can be drawn between the results presented in this thesis from acute hemilabyrinthectomized animals, the experiments of Miller et al. (1982), and the results of Maeda et al. (1975). Following lesions within the medulla to the lateral vestibulospinal tract or following high spinal hemisection the occurrence of synaptic events in contralateral motoneurones on labyrinthine stimulation is greatly reduced (Maeda et al., 1975). These results support the suggestion

that the pathway to contralateral motoneurones descends ipsilaterally in the cord before crossing. This pathway, deduced from the studies detailed in this thesis and from the results of Miller et al. (1982) can be identified as the contralateral beta mediated pathway. While the ipsilateral synaptic events observed by Maeda et al. (1975) correspond to the postulated ipsilateral beta and alpha pathways.

It would therefore appear that both the ipsilateral and contralateral pathways, which are thought to exist and participate in generating labyrinth reflexes onto extensors, can, by acting through spinal interneurones, utilize the lateral vestibulospinal tract. Maeda et al.(1975) demonstrated that both ipsi- and contralateral actions to forelimb motoneurones involve a trisynaptic link from the labyrinth, indicating that a spinal interneurone is interposed in both pathways. The simplest routes for these pathways have the folowing components (1) contralateral pathway: labyrinth- Deiters' nucleus (lateral vestibulospinal tract beta cells)- commisural spinal interneurone (excitatory)- contralateral extensor motoneurone, (2) ipsilateral pathways: labyrinth- Deiters' nucleus (lateral vestibulospinal beta and alpha cells)- spinal interneurone (excitatory)- ipsilateral extensor motoneurone. These pathways are not the only ways in which labyrinthine activity can reach the spinal cord. It is known from the work of Peterson et al. (1980) and Manzoni et al. (1983) that reticulospinal tract cells are responsive to electrical and natural labyrinthine

stimulation respectively.

Pompeiano (Manzoni et al., 1983) regards the reticular formation contribution to the development of labyrinth roll-tilt reflexes as one which compliments an ipsilateral vestibulospinal facilitation of extensors by altering levels of inhibition. Of the tilt sensitive cells located in the reticular formation the ratio of cells excited by side-up tilts to cells excited by side-down tilts is the inverse to that found within lateral vestibilospinal neurones (Manzoni et al., 1983). The distribution of tilt sensitive cells in the reticular formation is believed by Manzoni et al. (1983) to reflect the behaviour of contralateral vestibulo-spinal cells, and so during side-up tilts the activity in the majority of tilt sensitive reticular neurones will increase, while during side-down tilts their activity will fall. These cells are thought to provide extensor inhibition during side-up tilts and disinhibition on side-down tilts (Manzoni et al., 1983). The reticulospinal cells as described by Manzoni et al. (1983) can certainly assist in the development of labyrinth reflexes by modulating levels of inhibition to limb extensors, however this is not their only possible role. In particular the possible role of reticulo-spinal relations in developing the flexor component of the labyrinth reflex cannot be discounted.

4.3.2 Pathways that can mediate the flexor response to head rotation.

The results from experiments carried out on cats with intact labyrinths have demonstrated the following: (1) head rotation acts both on limb extensor and flexor musculature, and (2) in the normal animal these actions are organised reciprocally. The involvement of the flexor musculature in labyrinth and neck reflexes can be thought to operate through a number of hypothetical mechanisms, although from the experiments carried out, no definitive conclusion as to what pathway operates during these reflexes can be made. In this section of the thesis evidence supporting or attacking various ideas on the development of the flexor labyrinth reflex will be discussed.

The nature of the reciprocal organisation between flexor and extensor muscles conforms with the classical Sherringtonian concept of reciprocal innervation (Sherrington, 1892; see, Collected writings of Sir Charles Sherrington, 1979, Ch VII). One mechanism which could account for the behaviour of flexor muscles during head rotation would be that the descending labyrinthine input to extensors also acted upon interneurones mediating reciprocal inhibition of flexors. In such a scheme extensor facilitation would be accompanied by flexor inhibition (resulting from an increase in the drive to Ia inhibitory interneurones). Similarly a reduction in extensor facilitation (side-up tilt) would lead to a disinhibition of flexor motoneurones and this could lead to what appears like facilitation in the flexor EMG. In this mechanism, the flexor EMG will always reflect the inverse of the

excitatory drive to the extensor motor pools, although an increase in activity can only occur if the motoneurones are under some facilitation which is released following the removal of inhibition.

The observation that stimulation of the whole labyrinth induced IPSP's bilaterally in forelimb flexor motoneurones (Maeda et al. 1975) supports the idea that the flexor labyrinth reflex is mediated by modulation of an inhibitory mechanism. The inhibition occurs with a latency that requires four synapses, which is one more than is observed in the excitatory pathway to extensors (Maeda et al., 1975). Additional support comes from studies on descending inhibition of hindlimb flexors (Grillner et al., 1966), which demonstrate that electrical stimulation of Deiters' nucleus evokes a short latency IPSP in flexor motoneurones, and that subthreshold stimulation of this nucleus facilitates transmission of a submaximal Ia IPSP from quadriceps. Grillner et al. (1966) concluded that the vestibulospinal tract by utilising the reciprocal Ia inhibitory path can distribute inhibition to flexor motoneurones. This covergence of descending vestibulospinal volleys with extensor coupled Ia inhibitory interneurones has been confirmed by several studies investigating the time course of reciprocal Ia inhibition of hindlimb flexors (Grillner and Hongo, 1972; Hongo, Kudo & Tanaka, 1975; Hultborn and Udo, 1972a; Hultborn and Udo, 1972b), and by direct recording from the interneurones themselves (Hultborn, Illert & Santini, 1975). Indeed the lateral vestibulospinal tract is the only descending tract in the

cat known to project directly to Ia inhibitory interneurones (Baldissera, Hultborn & Illert, 1981).

In the discussion on pathways mediating the labyrinth reflex to extensors it was concluded that a contralateral pathway dominated over ipsilateral actions. Following hemilabyrinthectomy the flexor- extensor relationship of reciprocating activity is maintained in both limbs but the pattern in the limb contralateral to the lesion is reversed. It would, therefore, appear that the flexor responses follow the same hierarchical organisation as the extensor response does, that is, the normal response is dependant on the presence of the contralateral labyrinth. Again the results of Maeda et al. (1975) support this view. Vestibulo-spinal tract lesion abolishes IPSP's both ipsi- and contralaterally (Maeda et al., 1975) and so strengthens the case that inhibition from the contralateral labyrinth acts in flexor labyrinth reflexes. Similarly, Hongo et al. (1975) demonstrated in the hindlimb that crossed inhibition of flexor motoneurones resulting from vestibulospinal tract stimulation requires a neural circuit involving a commisural interneurone and a Ia inhibitory interneurone (see Fig. 101).

Although a mechanism of modulated inhibition with head tilts can theoretically provide the form of reflex reactions observed in forelimb flexors, alternative schemes can also be envisaged. There is evidence that the extensor and flexor responses can be generated independently of each other, which implies the absence of a shared descending influence and the presence, to some extent, of separate

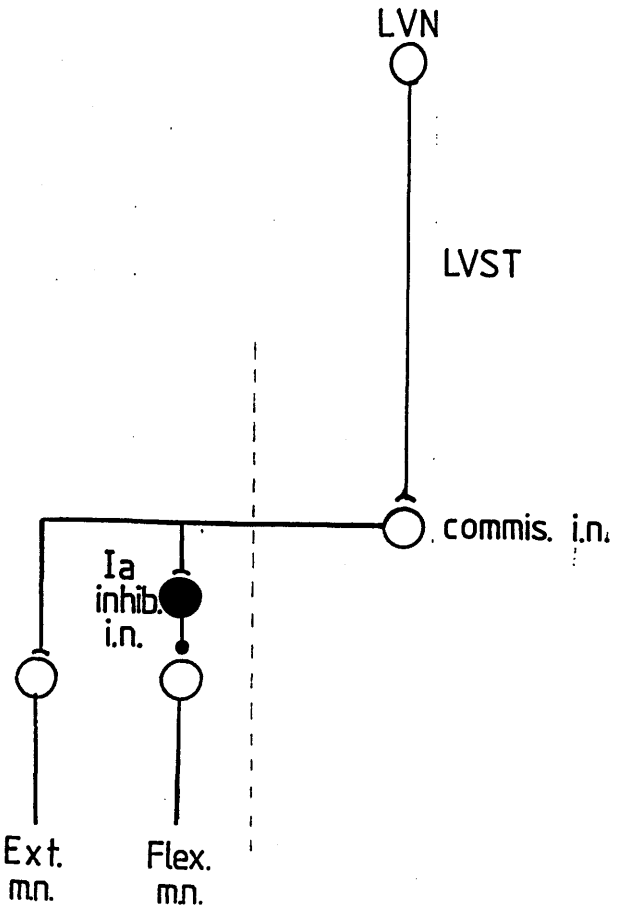


Figure 101. Inhibitory pathway from contralateral vestibular nuclei to limb flexor motoneurones. The inhibitory pathway from the contralateral lateral vestibular nucleus (LVN) to flexor motoneurones (flex m.n.) is mediated by convergence onto Ia inhibitory interneurones (Ia inhib. i.n.) from a commisural interneurone (commis i.n.) receiving synaptic input from the lateral vestibulospinal tract (LVST). This pathway represents a means whereby a reciprocal input to flexor and extensor (ext m.n.) motoneurones can operate.

"private" inputs.

In several instances labyrinth reflexes were observed to occur in flexor musculature when no EMG change could be observed in extensors. In this case, if the inputs to each motor pool reflected the inverse of the same descending influence, it would seem that reflex transmission must be dependant on the excitability of the interposed spinal interneurones, (alterations of which might occur in fluctuating levels of decerebrate rigidity). Though an equally valid hypothesis is that flexor and extensor activity result via modulation of 'independent' facilitatory systems which may also show suppression or enhancement of reflex transmission with altering levels of rigidity. The results of experiments in this thesis, although unable to prove this concept, can provide support for a scheme involving facilitatory pathways to flexors.

In several acute experiments the left flexor did not always respond in a reciprocal manner to activity changes in the left extensor. This observation, although occurring in a minority of experiments, suggests that an independent pathway to flexor motoneurones may be in operation, since such activity cannot be easily predicted from a model in which flexor activity during head tilts is dependant on altered levels of reciprocal inhibition.

If an excitatory projection exists from the labyrinth to flexor motoneurones, it is unlikely that it acts via vestibulospinal systems. In order to preserve the nature of the flexor response to head tilt and the reciprocal relationships between extensor and flexor

muscles the drive to the flexors during head tilt must reflect the inverse response to the drive to extensors. Afferent projections from the otoliths show a distribution of responses that can be characterised by increases or decreases in activity with lateral tilt. Within the lateral vestibular nuclei this distribution is preserved in the sense that the proportion of secondary vestibular neurones showing increased activity with side-down tilts (alpha response) to those that increase firing with side-up tilts (beta response) is the same as that found in the eighth nerve (for review see Goldberg and Fernandez, 1984). Recently, the response of reticulospinal neurones to lateral tilt has been recognized to reflect the opposite distribution of responsive units to that found within the ipsilateral eight nerve or lateral vestibular nucleus (Manzoni et al., 1983). These cells were described to be located, with topographical representation, within the medullary reticular region. Cells excited by side-up tilt were found in highest density in caudal most regions of the medullary reticular formation whilst units excited by side-down tilt were generally found in rostral regions of the explored reticular formation. Manzoni et al. (1983) concluded that macular signals exert selective control over limited regions of the reticular formation. Since these reticulospinal projecting cells behave in many ways opposite to vestibulospinal neurones of the same side, the possibility exists that these cells could participate in the generation of the flexor response to head rotation.

Sprague and Chambers (1954) in an early study on

the reticular formation demonstrated that electrical stimulation of different regions could induce alterations in postural tonus. Interestingly, it was observed that the most predominate effect of reticular stimulation on limb posture was of a reciprocal nature (Sprague and Chambers, 1954). If the stimulus was applied within medial regions ipsilateral flexion, and extensor inhibition was accompanied by contralateral extension and flexor inhibition, however if the stimulus was directed within lateral regions of the reticular formation then the opposite pattern of ipsilateral extension and contralateral flexion resulted. Widespread regions of the reticular formation therefore appear to be able to influence limb posture, and as these effects are predominately reciprocal between extensor and flexor the possibility of a reticulospinal contribution to labyrinth reflexes in flexor muscles cannot be excluded.

Lund and Pompeiano (1968) reported that extensor and flexor motoneurones in some hindlimb muscles received monosynaptic EPSP's upon stimulation of the brain stem. The excitatory influences on extensor motoneurones were recognised to be mediated by vestibulospinal systems, while the action on flexor motoneurones resulted from electrical stimulation outwith vestibular areas of the brain stem. Grillner and Lund (1968) in examining this excitatory descending pathway to flexor motoneurones discovered that monosynaptic descending effects to knee and ankle flexor motoneurones could be attributed to fibres descending in the medial longitudinal fasiculus. Grillner and Lund

(1968), on anatomical evidence, suggested that these fibres probably originated in the lower pontine reticular formation. The excitatory action onto flexors reflects a reciprocal organisation when compared to the action evoked by stimulating Deiters' nucleus. Stimulation of the medial longitudinal fasiculus also evokes inhibition of hindlimb knee extensors. On this basis Grillner, Hongo & Lund (1968) suggested that the vestibulo-spinal tract and the reticulospinal system are functionally coupled in the control of hindlimb motoneurones. Similarly, Wilson and Yoshida (1969) and Peterson, Pitts & Fukushima (1976) have reported, for the forelimb, that reticulospinal stimulation results in extensive direct excitation of elbow flexors, but not of elbow extensors. Within the reticular formation the effective sites for evoking monosynaptic actions to forelimb and hindlimb motoneurones correspond to the sites of origin of medial reticulospinal tract fibres, while stimulation of regions giving rise to the lateral reticulospinal tract do not produce short latency excitatory potentials in limb motoneurones (Peterson et al., 1976). It would therefore appear that cells located in the medial pontine reticular formation are capable of providing facilitation of elbow flexors.

Therefore, the reticulospinal system is capable of providing an excitatory input to limb flexor motoneurones, and there is also evidence that this system is reciprocally organised with respect to the vestibulospinal system (Grillner et al., 1968; Wilson and Yoshida, 1969). If the reticulospinal system is to participate in labyrinth

reflexes within forelimb flexors it is essential that a population of neurones projecting to flexors receives labyrinthine input. Manzoni et al., (1983) observed cells responsive to natural labyrinthine stimulation which are located mainly within medial portions of the reticular formation, and therefore may be considered as appropriate to mediate the labyrinth reflex to flexor muscles, (though the exact projection of these cells is unknown). Working with the hypothesis that these cells do act in generating labyrinth reflexes in flexor motoneurones the predominance of 'beta type' units (increased firing with side-up tilt) would require that these cells act ipsilaterally; unlike the beta cells located within Deiters' nucleus that are thought to act on the contralateral extensors. Although consistent with anatomical knowledge of reticulospinal systems (for review see Wilson and Peterson, 1981), an ipsilaterally descending pathway to flexor motoneurones must be able to operate within the known framework of labyrinth reflexes. For this reason it is necessary that tilt sensitive cells within the reticular formation receive their input from the contralateral labyrinth (as proposed by Manzoni et al., 1983, though for different reasons). In this way the pattern of labyrinth reflexes in the flexors of the acute hemilabyrinthectomized cats can be explained. The intact labyrinth will provide the normal input to the reticular formation on the side of the lesion and so evoke a normal reflex in the flexor of that side. A reversal of the reflex on the opposite side requires an ipsilateral projection from the labyrinth to the reticular formation in

parallel with that to the contralateral side. The ipsilateral action in the normal animal with intact labyrinths would be dominated by the contralateral labyrinthine input. The accompaning figures summarise this hypothetical organisation of labyrinth actions onto the flexors of the forelimbs. Fig. 102 illustrates the proposed ipsilateral and contralateral pathways to flexor motoneurones from the otolith and relaying through the vestibular nuclei and reticular formation. This figure depicts the situation one would find in an acute hemilabyrinthectomised cat where labyrinth reflexes are symmetrically organized. Additionally, given that in the acute preparation reflexes on the side of the lesion appear normal, then the relay to the contralateral reticular formation from the remaining labyrinth must be via cells in the lateral vestibular nucleus that increase their discharge with side-down tilts (alpha cells). In the intact cat with two functioning labyrinths the ipsilateral pathways are 'suppressed' and the contralateral pathways provide the labyrinthine input to the flexor motoneurones (see Fig. 103).

The labyrinth actions on forelimb flexors may be thought to result from both indirect (the result of modulation of inhibitory spinal mechanisms by vestibulospinal systems) and from direct pathways (via reticulospinal facilitation of flexor motoneurones). The two systems act to compliment each other in generating asymmetric and reciprocally organised labyrinth reflexes. The complete system (showing the major pathways to both

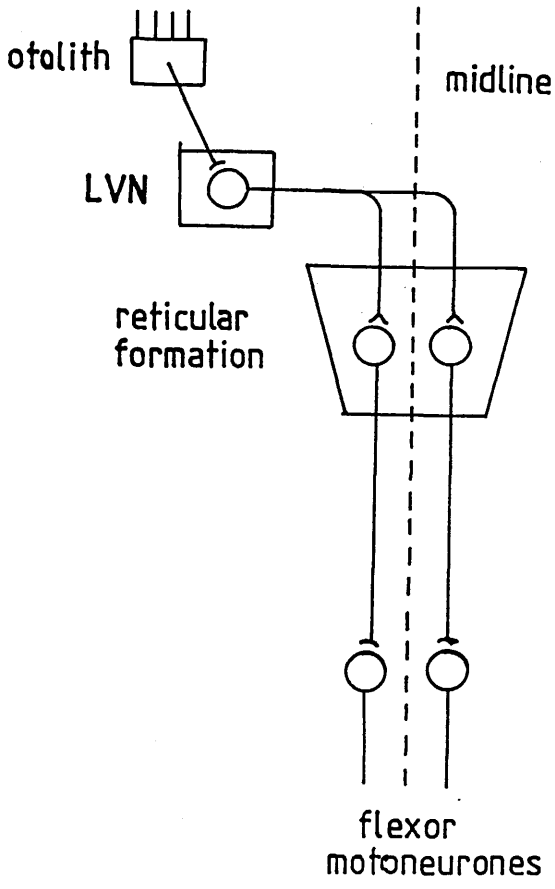


Figure 102. Proposed excitatory pathways from the otolith to flexor motoneurones relaying via the lateral vestibular nucleus (LVN) and the reticular formation. The pathways depicted in this figure are proposed in relation to the results from acute hemilabyrinthectomized cats and illustrate how symmetrical reflexes in the flexors from opposite sides can be generated.
(See text for description of these pathways).

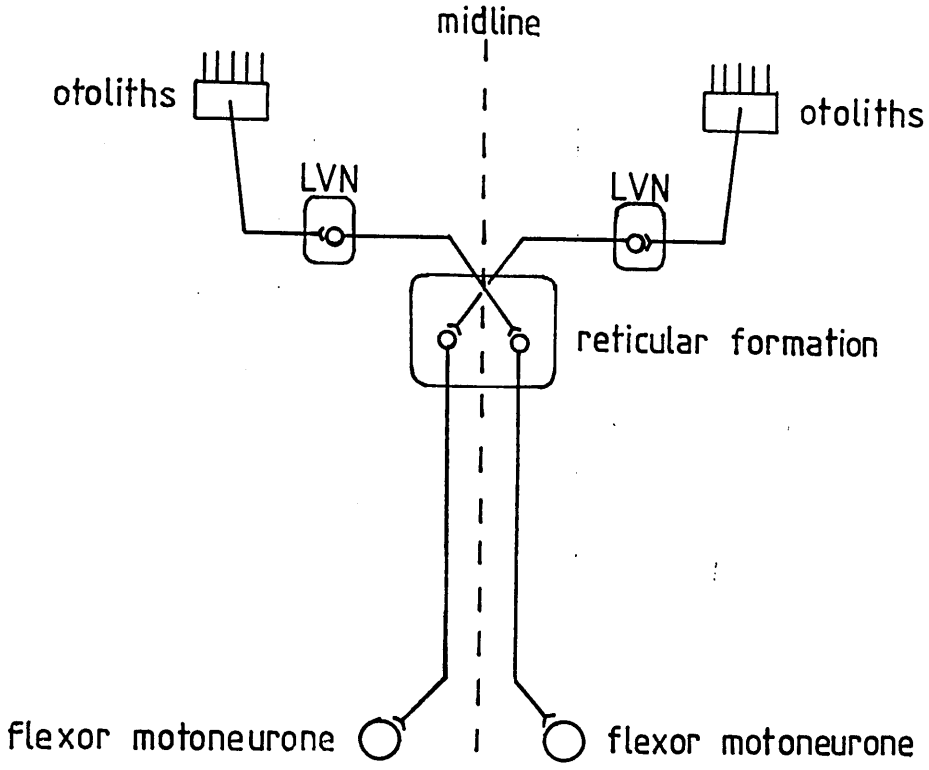


Figure 103. The proposed excitatory pathway to flexor motoneurones responsible for the appearance of normal labyrinth reflexes in these muscles. As with the pattern of extensor labyrinth reflexes in acute hemilabyrinthectomized preparations the labyrinth reflex in the flexor contralateral to the intact labyrinth appears normal. This requires that in the intact animal the proposed crossed pathway to flexor motoneurones is the dominant pathway in generating labyrinth reflexes in the flexors. It follows from this proposal that the reticular cells that project to the elbow flexors show an increased discharge on side-up tilts, which in turn requires that the input to these neurones from the contralateral lateral vestibular nucleus (LVN) is mediated by secondary vestibular neurones that show alpha discharge characteristics (i.e. increased output during side-down tilts). In this way normal flexor labyrinth reflexes can be expressed during head tilts.

extensor and flexor) is summarised in Fig. 104. This way of utilizing available pathways to extensors and flexors is only one possible way in which the labyrinth may evoke reflex actions onto limb motoneurones. Although highly speculative, the proposals made above indicate possible new avenues of research into the pathways mediating the tonic labyrinth reflex.

4.4.0 Limb somatosensory interaction with labyrinth and neck reflex actions.

Labyrinth and neck reflexes, as discussed previously, are believed to interact in such a way that postural stability is not threatened during voluntary head movements, and to provide appropriate compensatory reflex actions to stabilise posture during changes in attitude of support surfaces (Roberts 1978). As this model of postural control relies on the action of the labyrinths and neck proprioceptors on limb muscles it would seem reasonable to expect that limb attitude itself would be an important regulatory factor in this scheme.

Indeed, the results of experiments in this thesis have shown that changes in limb postion can modify the conditioning influence of the labyrinth and neck on the excitabilty of crossed extensor and flexor withdrawal reflexes. For example, altering the position of the limb affects the labyrinth and neck modulation of reflex excitability such that when the limb is extended flexor reflex excitability is greatest, while with the limb in

flexion, extensor reflex excitability is greatest (see Figs 69 & 70). Reflex excitability is therefore seen from these experiments to be a function of head, neck and elbow position. The somatosensory input from limb proprioceptors interacting with the descending labyrinth and neck signals to control reflex output.

Changes in limb position as carried out in this study are restricted to alterations in elbow joint angle about its natural axis of rotation. Alterations in the position of the elbow will result in a change in the discharge of slowly adapting mechanoreceptors located within the elbow joint capsule, and will also lead to a variation in the length of muscles that span this joint. It is therefore possible that any change in reflex excitability resulting form a change in elbow position may result from a modification of either elbow joint afferent or muscle afferent discharge.

Liddell and Sherrington (1925) in an investigation of tonic stretch reflexes reported that the strength of the reflex in quadraceps femoris varied with head position. Although this study did not investigate labyrinth and neck contributions independently, the result suggests that muscle afferents (involved in stretch reflexes) and descending proprioceptive input interact in the control of limb reflex output. Further support for this view was gained from the results of others (Denny-Brown, 1929; Kim and Partridge, 1969; Koella et al., 1956; Roberts, 1963; Rosenberg, Lindsay & Logan, 1980) who demonstrated that tonic stretch and vibration reflexes could be influenced by

independent natural labyrinthine or neck stimulation. It may be concluded from these studies that, as changes in elbow joint angle impose length changes on the muscles around the elbow, this would result in a propriceptive input capable of modulating the conditioning influences from the labyrinthine and neck.

Intra-articular injection of local anaesthetic is recognised as an effective means of selectively silencing joint afferent mediated discharge (Baxendale and Ferrell, 1981, 1982, 1983), but should not affect other nearby structures (Ferrell, Baxendale, Carnachan & Hart, 1985), and therefore will not influence muscle afferent discharge. Interestingly, modulation of reflex excitability with alterations in elbow position is lost following intra-articular injection of anaesthesia. This result implies that the modulation of reflex excitability from the limb is independent of muscle afferents. Despite previous studies demonstrating convergence between muscle afferents and descending labyrinth or neck afferences by muscle stretching (Denny-Brown, 1929; Kim and Partridge, 1969; Koella et al., 1956; Liddell and Sherrington, 1925; Rosenberg et al., 1980; Roberts, 1963), and by monosynaptic reflex testing (Wenzel and Thoden, 1977; Wenzel, Thoden & Frank, 1978) no such convergence is revealed in the present experiments following joint anaesthesia. It would therefore appear that there is no evidence to suggest that labyrinth and neck conditioning influences are altered by changes in muscle length. In this study movements of the limb about the elbow invlove length changes in antagonist muscle

groups whereas in previous studies length changes were restricted to single tenotomised muscles. The more natural movements employed in this study may therefore explain why no apparent contribution from muscle receptors was observed. The results presented in this thesis suggest that the effects resulting from changing elbow position are attributable to the activity in articular mechanoreceptors and not to muscle afferent activity.

One may assume that the modulation of reflex excitability is due to the interaction of labyrinth, neck and elbow joint afferents. However, the sites or locations of this interaction remain unknown. Although no indication of the location of this interaction can be made from the present experiments, several possible sites can be identified on the basis of other studies. One possible site of interaction is the vestibular nuclear complex. Cells within this region have been demonstrated to receive a somatosensory input which closely corresponds with the behaviour of slowly adapting joint receptors (Fredrickson et al., 1966; Rubin et al., 1977). These units, although responsive to limb position, never displayed a response to cutaneous stimulation or muscle pressure (Fredrickson et al., 1966). Rubin et al. (1977) observed that the majority of these 'joint modulated' units were found within the lateral vestibular nucleus, which is recognised to be an important site for the integration of labyrinthine and neck proprioceptive inputs (Boyle and Pompeiano, 1980, 1981; Brink et al., 1980; Mergner, Anastasopoulos, Becker & Deecke, 1981). It is therefore possible that regulation of

descending vestibular and neck conditioning influences to limb motoneurones can occur within the vestibular nuclear complex. It is also possible that the interaction between labyrinth, neck and joint proprioceptive inputs occur at the spinal level either by convergence onto a common interneurone or upon the motoneurones themselves. Joint afferent projections to motoneurones may set the excitability of a species of motor cells which then receive facilitation or inhibition from descending labyrinth and/or neck inputs, or similarly covergence may occur before the motoneurone onto interneurones that are known to recieve vestibular and neck afferents (Wilson et al., 1984).

Although the site of interaction between the separate afferent systems is not yet clear, a functional role for this convergence of joint mechanoreceptors with labyrinth and neck reflex systems can be incorporated easily into one model of postural control. The joint afferents provide the somatosensory information required by the central nervous system to allow the development of labyrinth and neck reflexes appropriate for postural stabilisation at any particular combinations of limb positions. The regulation or perhaps "gain control" over labyrinth and neck reflex expression in flexors and extensors occurs independently of muscle receptor discharge. We assume therefore that joint afferent discharge can regulate the reflex output of labyrinth and neck reflex systems to ensure that during a threat to stability compensatory reflexes are not stereotyped but are adjusted to be correct for the attitude of the animal.

4.5.0 Compensation to hemilabyrinthectomy.

Under normal circumstances given sufficent time the postural deficiencies resulting from unilateral labyrinthectomy are adequatly compensated for. Early studies on mammalian vestibular physiology recognized the presence of a compensatory mechanism (see Camis, 1930; Schaefer and Meyer, 1974). Nevertheless, there has been little attempt to study the form of labyrinth and neck reflexes in animals subsequent to hemilabyrinthectomy. Lindsay and Rosenberg (1978) however, demonstrated that the form of the labyrinth reflex in forelimb extensors eight weeks after unilateral labyrinthectomy was identical to that described for extensor muscles in cats with intact labyrinths. Rosenberg (unpublished observation) showed that the progress of the re-establishment of the normal form of the extensor reflex involves a plastic and adaptive change in the muscular response to head tilt in the limb extensor on the side of the remaining labyrinth. One aspect of postural compensation was therefore recognised as the return to normal of the labyrinth reflex in the limb contralateral to the damaged labyrinth. This re-establishment of normal head positional reflexes appears to provide the nescessary substrate for the operation of a stabilizing reflex interaction with neck positional reflexes. However, if one takes into consideration the participation of flexor muscles in labyrinth reflexes in these animals exhibiting a recovery of extensor labyrinth

reflexes, then an entirely different scheme for providing postural stability in the compensated cat must be proposed.

The new scheme of positional reflexes in the compensated cat is detailed in table VI, where comparisons can be made between labyrinth and neck reflex organisation in normal, acute and compensated cats. The most striking difference between the organisation of reflexes in normal and compensated animals is the appearence in the compensated state of parallel activity changes in the left extensor and flexor mucsles (ipsilateral to the initial lesion). This behaviour results from a reversal in the behaviour of the left flexor to head and neck rotations during the period of compensation. The behaviour of other muscle groups in the compensated animal show identical labyrinth and neck reflexes to those recorded in normal animals. For example, the direction of labyrinth reflexes seen in the right extensor and flexor of acute hemilabyrinthectomized animals return once more to a normal form. Thus in the compensated cat the reflex organisation to all muscle groups, except the left extensor, is altered by the compensatory mechanism. The left extensor muscle group is the only group to show no alteration in the direction of labyrinth and neck reflexes in normal, acute and compensated animals.

The compensatory process therefore operates to re-establish normal labyrinth/neck relations in the right limb, and restore the normal reflex antagonism between these two systems. (The disrupted labyrinth and neck reflex interactions seen in the right limb of acute animals are no

longer observed). In the left limb (which in the acute animal shows normal labyrinth and neck reflex interactions) the compensatory process acts to establish a reversed labyrinth and neck reflex in the flexor. The reflex reversal of both labyrinth and neck reflexes in the left flexor provides a strategy which preserves the antagonism between labyrinth and neck actions.

If compensatory mechanisms are related to regaining postural control, can the reflex system described above achieve this? By considering the extensors of the left and right sides, the labyrinth and neck reflexes are the same as those observed in the normal animal, and their interactions are compatible with theories where labyrinth and neck reflexes act to stabilise the position of the trunk (Lindsay et al., 1976). Regarding the relationship between extensor and flexor in the right limb the interactions between labyrinth and neck actions are also as described in the normal animal. However, the normal strategy for stabilization does not appear to operate in the right limb, where extensor and flexor act synergistically. One of the symptoms of hemilabyrinthectomy is a loss of extensor tone on the side of the lesion and it may be that the reversal in the labyrinth and neck reflex in the left flexor is designed to overcome this deficit. The reduced extensor tone on the side of the lesion may result in labyrinth or neck reflexes in the left extensor being inadequate to generate sufficient extra 'tone' to provide effective compensatory reflexes. By coactivating the extensor and flexor this situation can be overcome.

Activity generated within the normally antagonist muscles now acts to effectively increase the stiffness of the limb and thereby provide an output that can effectively compensate for larger loads than could be accomplished by the extensor and flexor acting in a strictly reciprocal fashion. Postural compensation can therefore be recognised to act not only to re-establish normal reflex interactions within the right limb, but can also be seen to reorganise labyrinth and neck reflexes within the left limb to overcome a deficiency in extensor tone within this limb. In the limb contralateral to the original lesion, labyrinth and neck reflexes regulate the distribution of tone between antagonist muscle groups (as in the normal cat), while ipsilateral to the lesion the stiffness of the limb is regulated by the level of coactivation of antagonist muscle groups. The compensated animal, despite the previous loss of one labyrinth, therefore, has the ability to generate compensatory labyrinth and neck reflexes which can operate together to provide effective trunk stabilisation.

In recent models of vestibular compensation, the compensatory process is believed to involve the restoration of symmetry between opposite vestibular nuclei by means of commisural connections within the brain stem and possibly the cerebellum (Galiana, Flohr & Melvill Jones, 1984). The absolute values of commisural gains are thought to affect the resting level of vestibular nuclear activity and compensation results from an imbalance in the gain of these commisural pathways. The structure of thier model is based on the known commisural pathways between vestibular nuclear

cells recieving canal input, while the operation of the model relies on experimental observations concerning vestibulo-occular compensation, as well as the recovery of head tilt following hemilabyrinthectomy. Without needing to give a lengthy discussion of this model it is clear, that despite the authors belief in the Galina model as a mechanism of postural as well as ocular compensation, the model cannot be used to explain the reorganisation of the postural reflexes that are described in this thesis. Indeed, since the evidence on which Galiana et al. (1984) base their views on postural compensation aries from the work of Flohr, Bienhold, Abeln and Mackovics (1981) on the compensation of head tilts in frogs, it does not seem appropriate to apply this situation to that seen in cats. In my own experience the head tilt in cats is one aspect of labyrinthectomy that is not compensated for -in one cat head tilt was apparent even eight months after hemilabyrinthectomy (an observation also made by Camis, 1931). Postural compensation as described in this thesis is not simply the re-establishment of symmetry between opposite sides but involves a complex reorganisation of labyrinth reflexes to both sides, and also the modification of the neck reflex to the side of the lesion. As little is known about this reorganisation of limb reflexes, the compensatory process that acts to provide it can only be guessed at.

Some evidence does, however, suggest that postural compensation is dependent on structures other than those involved in occular compensation. The reappearance of

nystagmus in compensated animals upon decerebration (Dutia and Rosenberg, 1981) support this view. It appears therefore that occular compensation is dependant upon centres outwith the brain stem, whereas postural compensation may be a feature of structures located in the brain stem and possibly the spinal cord. Although it seems reasonable to suggest that the re-establishment of vestibular nuclear activity seen following vestibular lesions (Precht et al., 1966; Pompeiano, Xerri, Gianni & Manzoni, 1984) is intimately concerned with the process of compensation, the re-organisation of the pattern of labyrinth reflex in chronic animals, and the reappearance of nystagmus following decerebration indicates that this is not the only contributing factor to the compensatory process. Compensation is clearly a process that is more complex than first envisaged.

4.6.0 General discussion and concluding remarks.

The experiments presented in this thesis provide an examination of the organisation of labyrinth and neck reflexes in normal cats, and also in cats subjected to hemilabyrinthectomy (acute and chronic).

In the normal animal with intact labyrinths the reflex scheme presented supports and extends pre-existing theories (Lindsay et al., 1976) on the involvement of labyrinth and neck reflexes in the control of posture. By demonstrating the participation of limb flexors in labyrinth and neck reflexes and the existence of a specific

reciprocal relationship to extensor induced motor activity, the pattern of naturally evoked reflexes is suggestive of two opposing systems (labyrinth and neck) that act independently on the distribution of tone within antagonist muscles of a limb. From a functional point of view this implies that when one system is brought in to play the posture of the limb is determined by the balance between activity in the extensor and flexor. In addition, the demonstration that limb postion can regulate the reflex output of the limb, and condition descending labyrinth and neck reflex influences, ensures that during the execution of a labyrinth or neck reflex the muscular output is tailored to the exact requirements needed to meet the postural requirements of the animal. Thus (in agreement with Lindsay et al., 1976) when labyrinth and neck reflex systems are brought synchronously into play the subsequent interaction of these reflex systems result in no net reflex output, and so allows movements of the head to occur upon a stable postural base; though when evoked separately the expression of the labyrinth or neck reflex is sufficent to compensate for the disturbance evoking the reflex in the first place.

Support for the above reflex system operating in the normal animal comes from the results of experiments carried out on acute hemilabyrinthectomized animals. In the acute animal, the disturbance to the organisation of labyrinth reflexes result in an abnormal interaction with neck reflexes, which in part accounts for the behavioural disturbances in posture seen in these animals. These

deficits, are recognizable as an inability to correctly adjust limb position during imposed tilts of the supporting surface or to stabilise body position during head movements. The abnormal interactions are the result of a reversal of the labyrinth reflex contralateral to the lesion. While ipsilateral to the lesion the reflex appears normal a result which is strongly indicative that the normal labyrinth reflex is dependant on the integrity of the contralateral labyrinth. Although the result of hemilabyrinthectomy imposes severe postural disabilities on an animal, a remarkable process of compensation to the lesion occurs. This compensation involves plastic and adaptive modifications to the acute pattern of labyrinth and neck reflexes and illustrates how the surviving labyrinth can provide, along with the neck proprioceptors, a scheme of reflexes which, although essentially different from the scheme described for cats with intact labyrinths, acts to provide the same end result.

Appendix A.

This appendix in conjuction with methods section (chapter 2) provides a dissection guide for the denervation of the atlanto-occipital and atlanto-axial joints. The appendix consists of a series of photographs and accompanying line drawings which illustrate various steps in the dissection. The photographs were obtained from a dead animal.

Plate AI illustrates the surface of the muscles of the back of the head and neck on retracting the skin.

Plate AII illustrates the deeper muscles of the neck after the retaction of the superficial muscles, the spinal process of the axis is clearly visible in this plate.

Plate AIII, in this plate the muscles surrounding the axis vertebra have been partially cleared.

Plate AIV, this plate shows the extent to which the muscles surrounding the axis and atlas vertebrae have to be cleared and the exits of the C1 and C2 spinal nerves can be clearly seen.

Plate AV, in this plate the dorsal and ventral roots of one of the C2 spinal nevres has been cut proximal to the dorsal root ganglia.

Plate AVI in this plate both C2 spinal nerves have been sectioned.

Plate AVII following the denervation of the atlano-occipital joint a portion of the dorsal surface of

the atlas is removed to facilitate access to C1 dorsal roots.

Plate AVIII, this plate illustrates how after opening the dura and lifting it the C1 dorsal roots can be easily exposed and then sectioned.

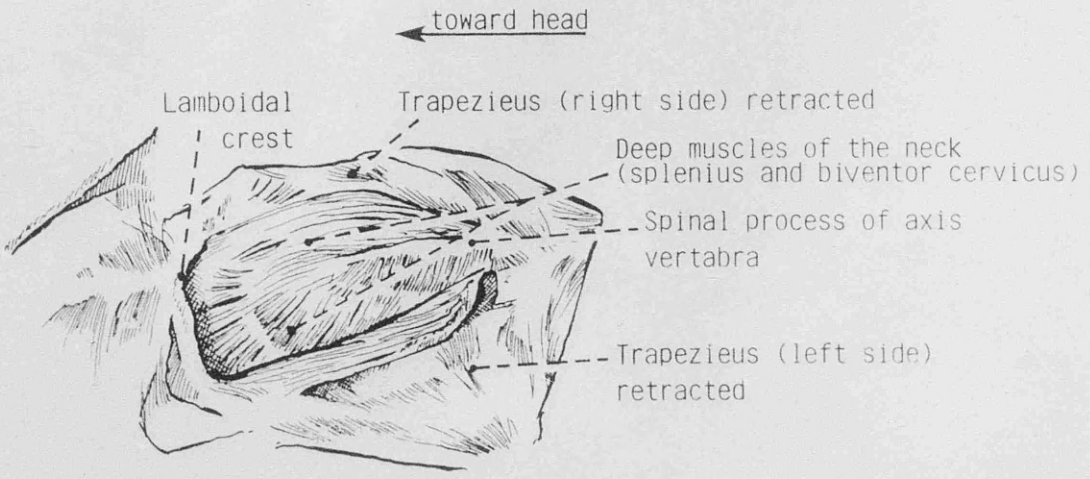

toward head
Lamboidal crest
Trapezieus (right side) retracted
Deep muscles of the neck (splenius and biventor cervicus)
Spinal process of axis vertabra
Trapezieus (left side) retracted

Plate AI.

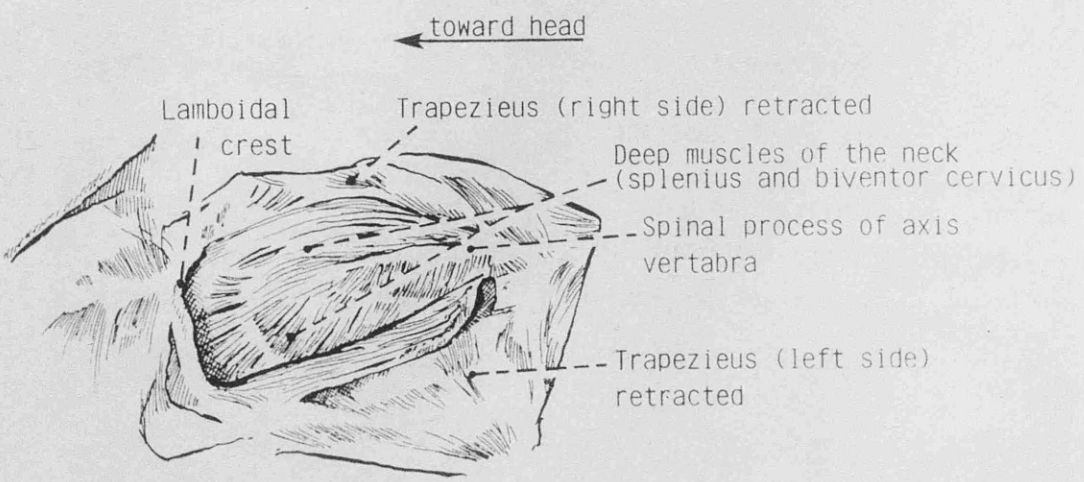

toward head
Lamboidal crest
Trapezieus (right side) retracted
Deep muscles of the neck (splenius and biventor cervicus)
Spinal process of axis vertabra
Trapezieus (left side) retracted

Plate AII.

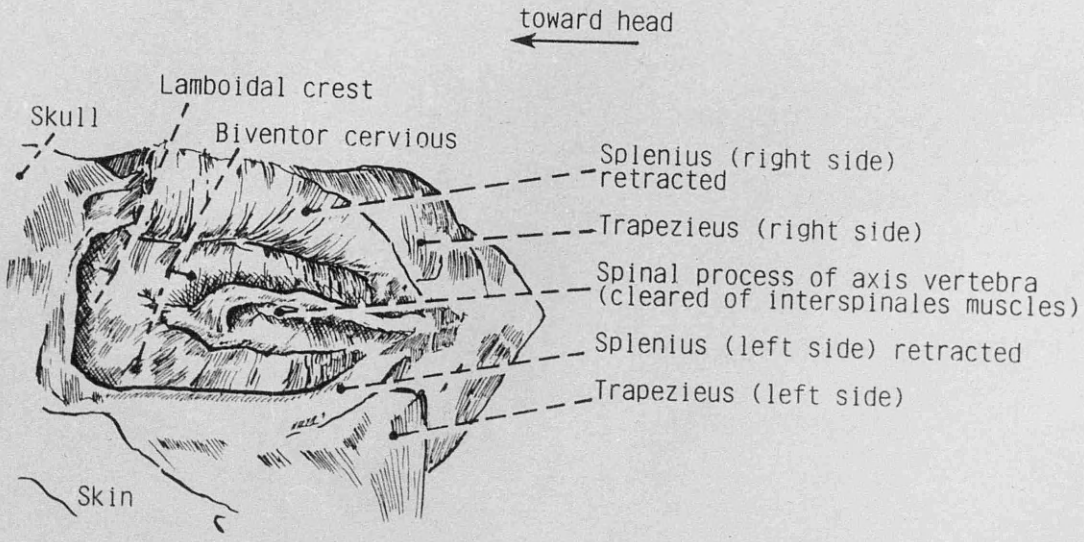

toward head
Lamboidal crest
Skull
Biventor cervious
Splenius (right side) retracted
Trapezieus (right side)
Spinal process of axis vertebra (cleared of interspinales muscles)
Splenius (left side) retracted
Trapezieus (left side)
Skin

Plate AIII.

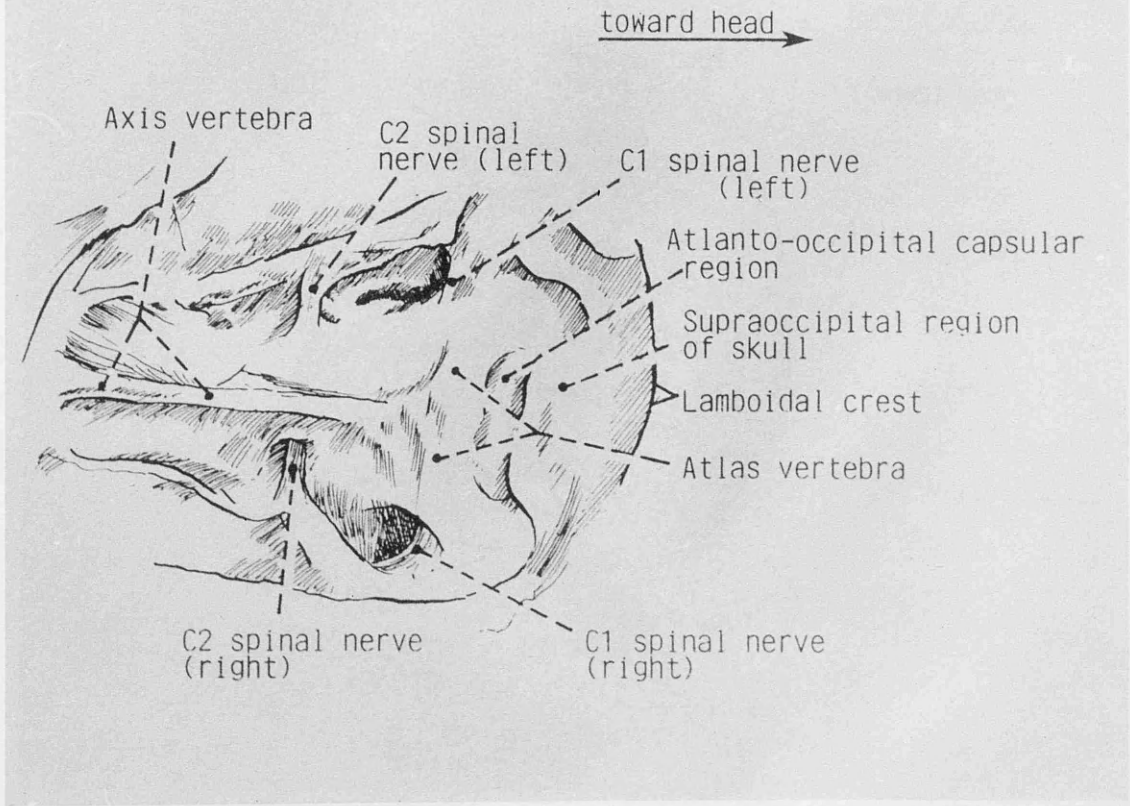
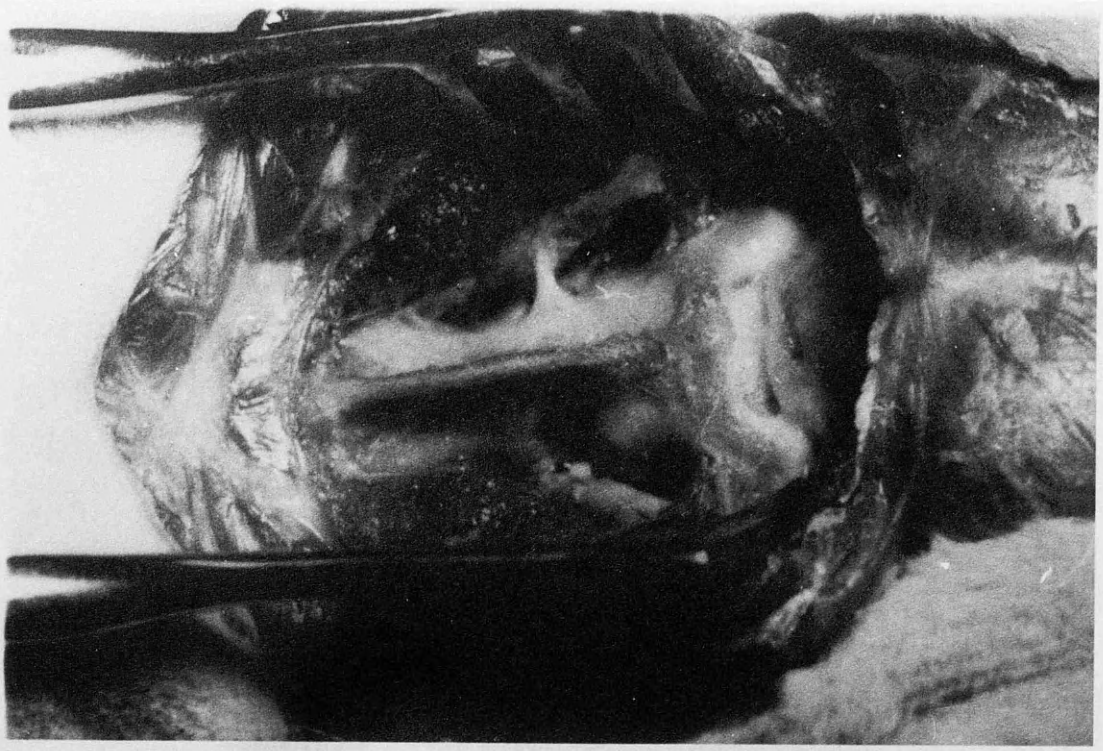

toward head
Axis vertebra
C2 spinal nerve (left)
C1 spinal nerve (left)
Atlanto-occipital capsular region
Supraoccipital region of skull
Lamboidal crest
Atlas vertebra
C2 spinal nerve (right)
C1 spinal nerve (right)

Plate AIV.



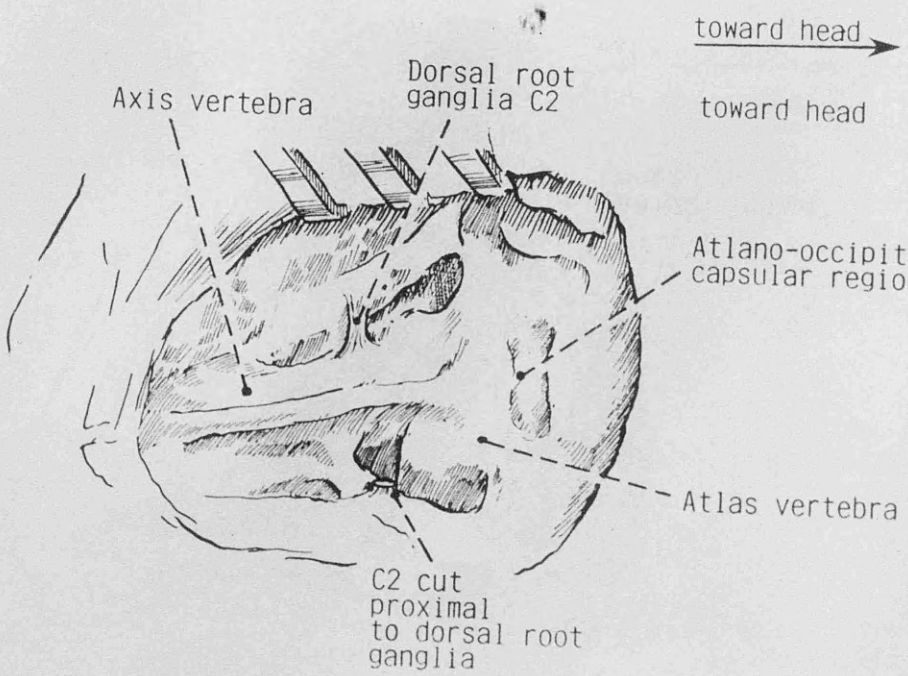
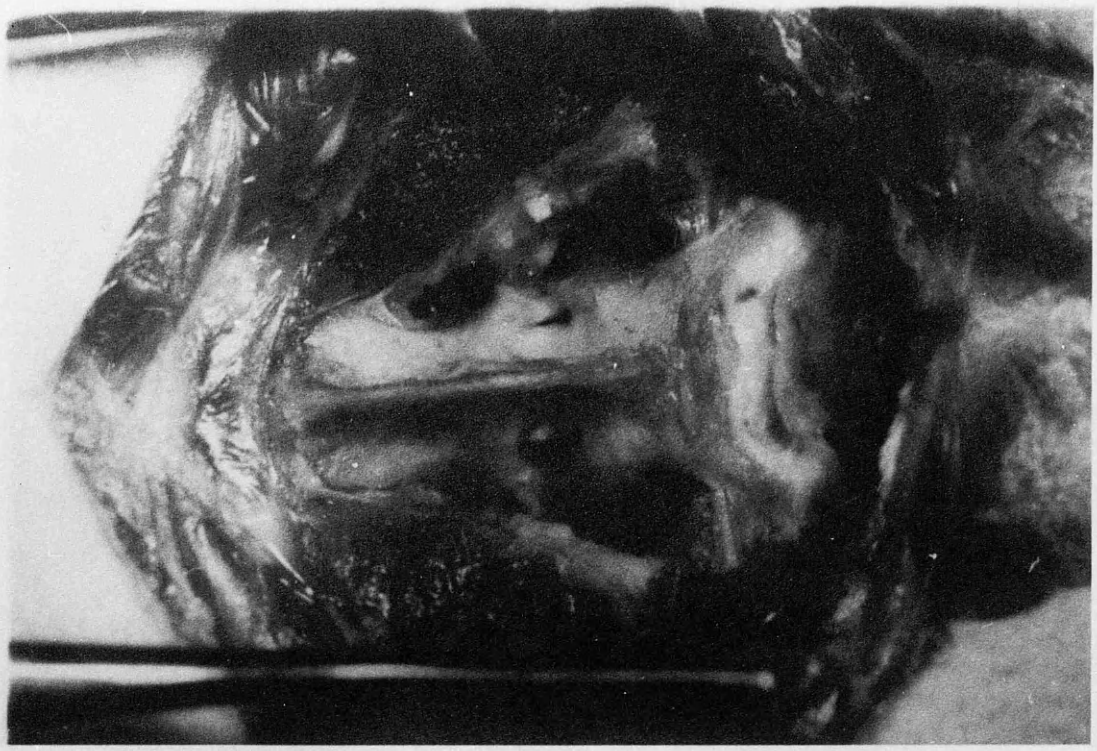

toward head
Dorsal root ganglia C2
Axis vertebra
toward head
Atlano-occipital capsular region
Atlas vertebra
C2 cut proximal to dorsal root ganglia

Plate AV.



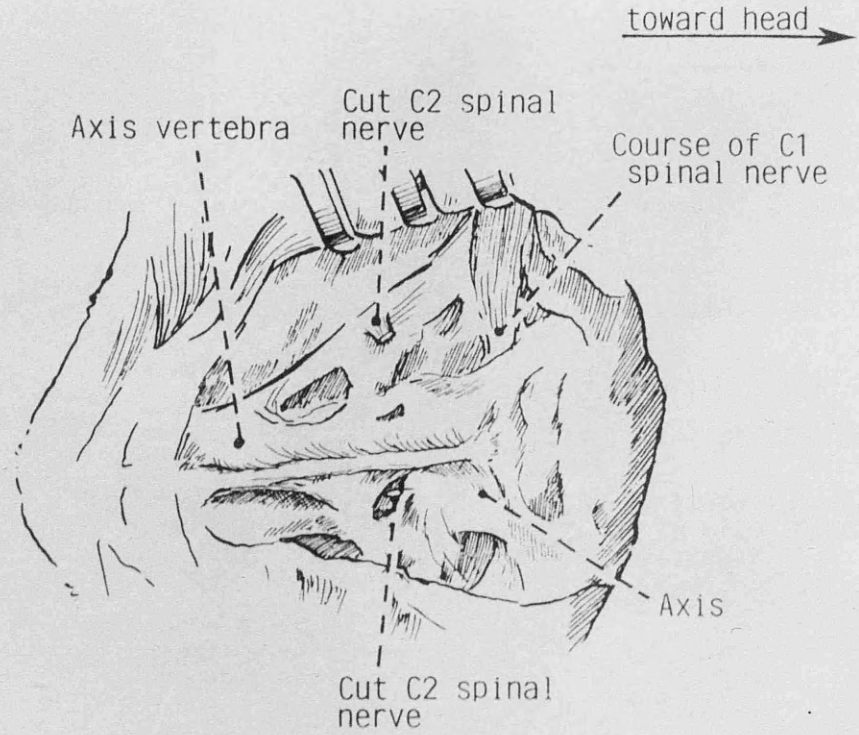
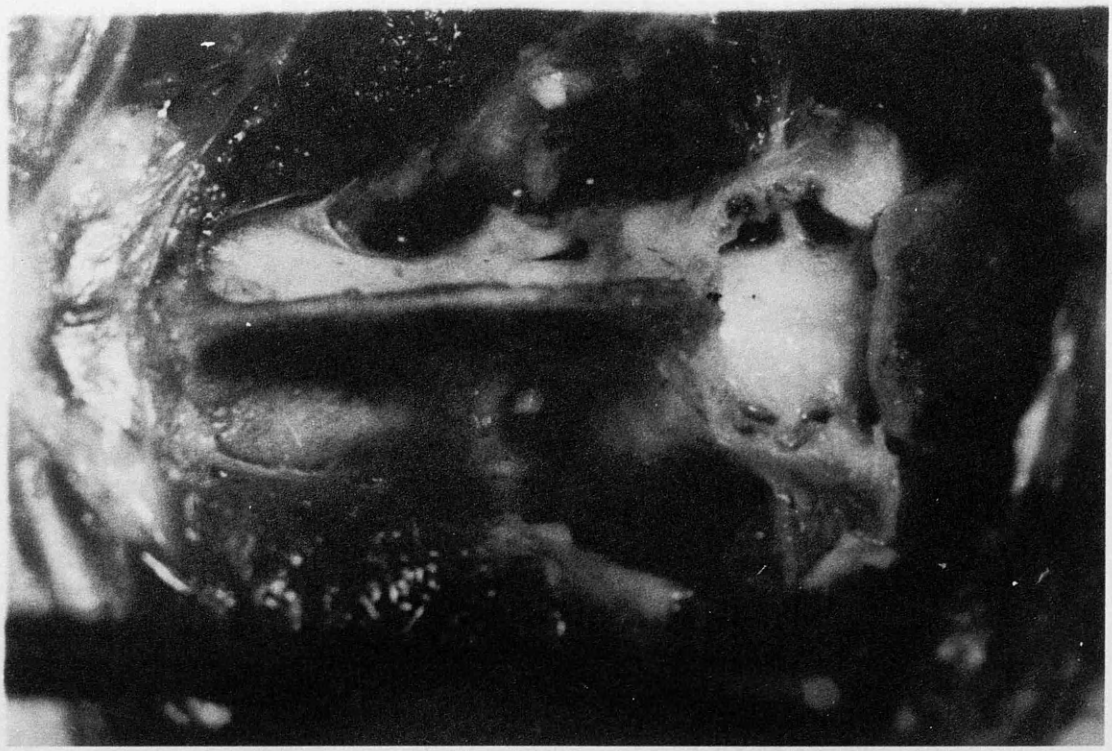

toward head
Axis vertebra
Cut C2 spinal nerve
Course of C1 spinal nerve
Axis
Cut C2 spinal nerve

Plate AVI.



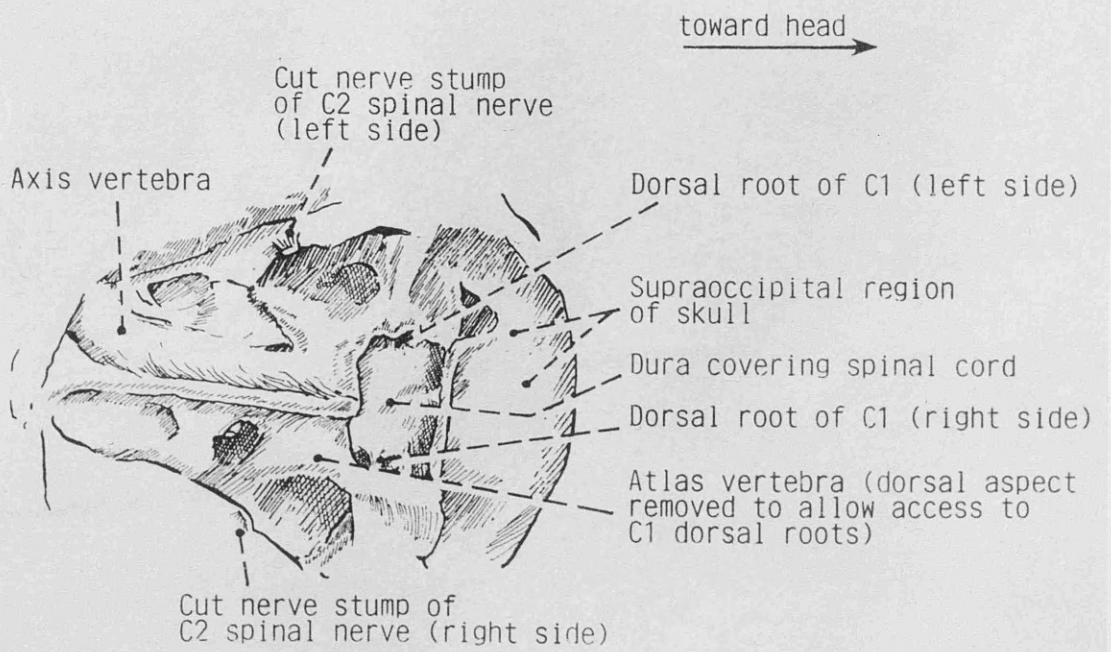
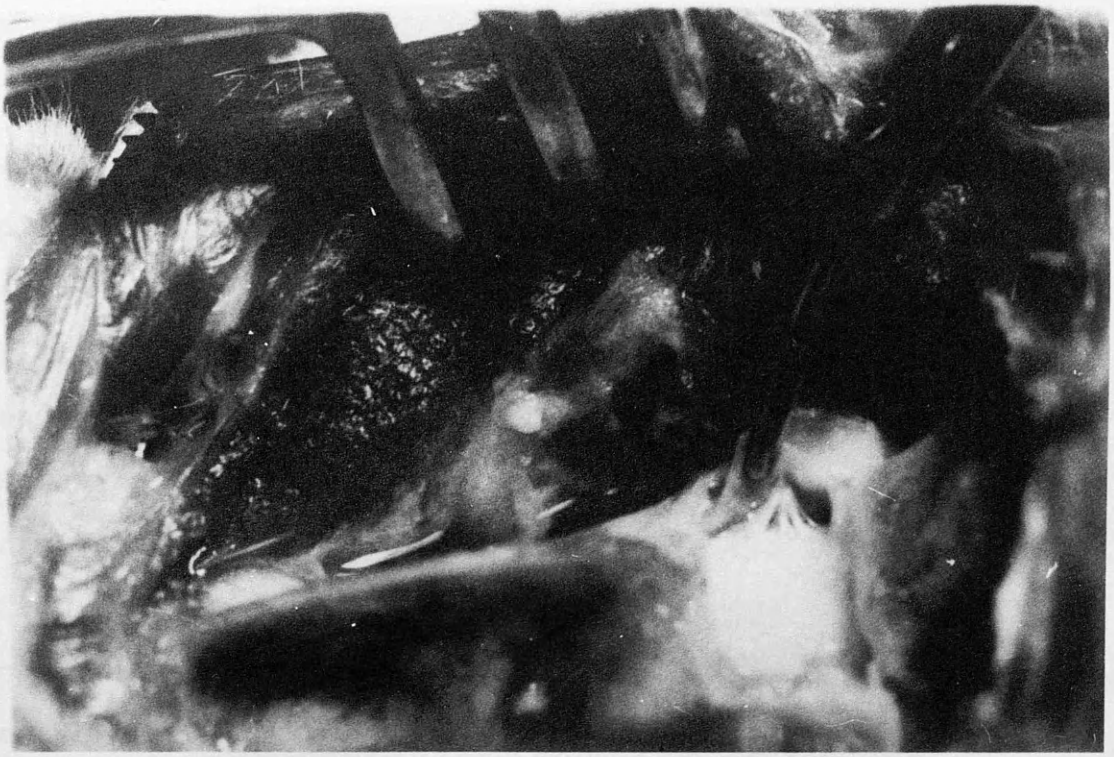

toward head
Cut nerve stump of C2 spinal nerve (left side)
Axis vertebra
Dorsal root of C1 (left side)
Supraoccipital region of skull
Dura covering spinal cord
Dorsal root of C1 (right side)
Atlas vertebra (dorsal aspect removed to allow access to C1 dorsal roots)
Cut nerve stump of C2 spinal nerve (right side)

Plate AVII.



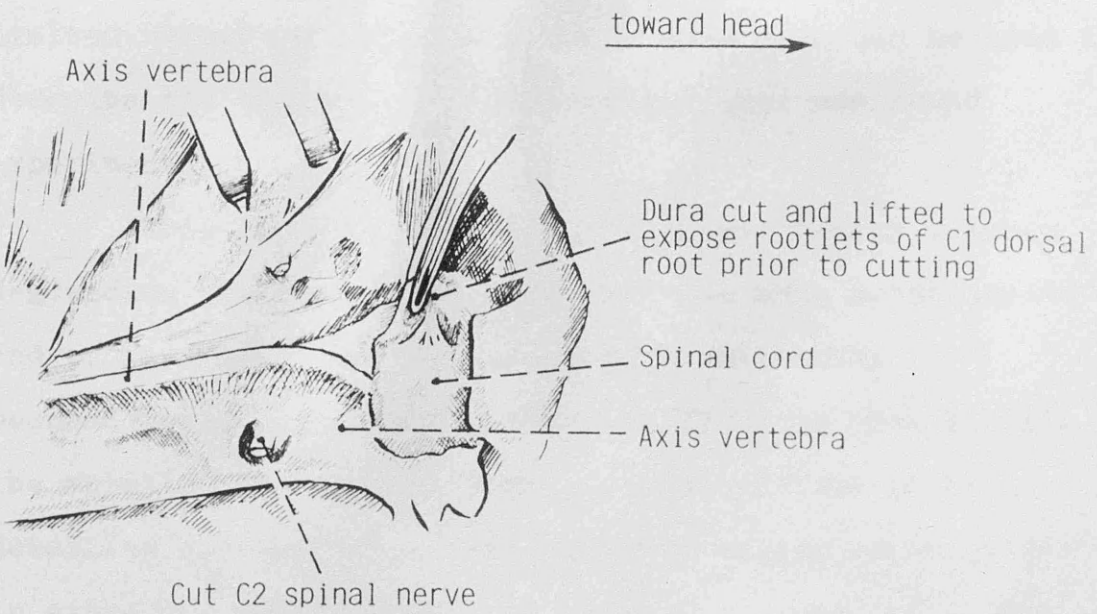

toward head
Axis vertebra
Dura cut and lifted to expose rootlets of C1 dorsal root prior to cutting
Spinal cord
Axis vertebra
Cut C2 spinal nerve

Plate AVIII.

Appendix B.

Changes in head or neck position, as well as alterations in elbow joint position have been shown to alter segmental reflex threshold in very specific ways. For example, graphs showing crossed extensor and ipsilateral flexion reflex threshold modulation with changes in head and elbow position (Figs 77a & b, 78, 79) and neck and elbow position (Fig 77b) have characteristic shapes which are related to the type of muscle and the limb recorded from. The object of this appendix is simply to identify operations that can transform the results pertaining to one set of conditions to those of another. For example, is there a simple operation that would carry the surface shown in Fig 77a to that of Fig 77b. More generally, are there a limited number of elementary operations that can be used to describe the variety of relationships that are found experimentally.

This appendix examines the relationships between descending (labyrinth and neck) actions onto motoneurones and of peripheral actions mediated by articular mechano-receptors. The experimental findings that provide the material for this appendix are gained from sections detailing the modulation of segmental reflex excitability in extensors and flexors with changes in head, neck and elbow joint position (3.5. & 3.6).

From the three dimensional graphs (e.g. Fig 77a & b, 78, 79), used in section 3.5, it is clear that the surfaces defined conform to one of four possible options,

defined in terms of the corner in which the peak of the graph occurs.

By looking down onto such graphs the data contained within them can be expressed by square matrices. The position of an element within a row of such a matrix idicating head position, while column position signifies the attitude of the limb. The absolute value of a particular element expressing reflex threshold at a combination of limb and head or neck positions (see below).

				LIMB POSITION
	X	Y	Z	FULL EXTENSION
	M	N	O	MID RANGE
	A	B	C	FULL FLEXION
HEAD OR NECK POSITION	LEFT SIDE DOWN	MID POSITION	RIGHT SIDE DOWN	

If each element in the above matrix is given a specific magnitude then the matrix will conform with the experimental observations if we assume that X is greater than the others and C has the smallest magnitude. By doing this, and scaling the other elements appropriately then a surface sloping away from the peak X monotonically to a minimum at C can be pictured. By doing this four matrices can be composed that define the peak of the graph in each of the corners of the grid shown above. These matrices are given below:

$$P = \begin{pmatrix} X & Y & Z \\ M & N & O \\ A & B & C \end{pmatrix} \qquad R = \begin{pmatrix} Z & Y & X \\ O & N & M \\ C & B & A \end{pmatrix}$$

$$S = \begin{pmatrix} C & B & A \\ O & N & M \\ Z & Y & X \end{pmatrix} \qquad T = \begin{pmatrix} A & B & C \\ M & N & O \\ X & Y & Z \end{pmatrix}$$

By studying the composition of these matrices it is seen that in comparing P to R (or S to T) that R (T) is gained by interchanging columns 1 of P (S) with column 3. Furthermore in comparing P to T (or R to S) it is evident that in these relationships interchanging rows 1 and 3 will map P onto T or T onto P (R onto S or S onto R). It therefore appears that by carrying out column or row operations, or combinations of both that any of the above matrices can be obtained from one of the others. When dealing with square matrices operations are described which carry out the above column or row switches. These operations are given below.

Column operations; in any 3 x 3 square matrix, post-multiplication with the permutation matrix E (defined below) interchanges columns 1 and 3.

Row operations; in any 3 x 3 square matrix, pre-multiplication with the permutation matrix E interchanges rows 1 and 3.

$$E = \begin{pmatrix} 0 & 0 & 1 \\ 0 & 1 & 0 \\ 1 & 0 & 0 \end{pmatrix}$$

Given the four basic matrices defined above (P, R,

S, T) it is possible to identify each with particular experimental conditions and define relationships between different conditons. By considering the actions of head, neck and elbow position on the excitability of limb motoneurones the above matrices are associated with the conditions outlined below.

P - Right triceps excitability changes with head and elbow position
  - Left triceps excitability changes with neck and elbow position

R - Right triceps excitability changes with neck and elbow position
  - Left triceps excitability changes with head and elbow position

S - Right flexor excitability changes with head and elbow position
  - Left flexor excitability changes with neck and elbow position

T - Right flexor excitability changes with neck and elbow position
  - Left flexor excitability changes with head and elbow position

If we consider the matrix P and examine the result of post-multiplication with E then it is clear that this operation relates: (1) Labyrinth and neck actions to a common muscle, and (2) relates labyrinth or neck actions to extensors or flexors from opposite limbs. This relationship

is defined below using P as an example.

$$P \times E = \begin{pmatrix} XYZ \\ MNO \\ ABC \end{pmatrix} \times \begin{pmatrix} 001 \\ 010 \\ 100 \end{pmatrix}$$

$$= \begin{pmatrix} (Xx0)+(Yx0)+(Zx1) & (Xx0)+(Yx1)+(Zx0) & (Xx1)+(Yx0)+(Zx0) \\ (Mx0)+(Nx0)+(Ox1) & (Mx0)+(Nx1)+(Ox0) & (Mx1)+(Nx0)+(Ox0) \\ (Ax0)+(Bx0)+(Cx1) & (Ax0)+(Bx1)+(Cx0) & (Ax1)+(Bx0)+(Cx0) \end{pmatrix}$$

$$= \begin{pmatrix} Z & Y & X \\ O & N & M \\ C & B & A \end{pmatrix} = R$$

In the same way R post-multiplied by E gives P, and S post-multiplied by E gives T.

$$R \times E = P$$
$$S \times E = T$$
$$\text{and } T \times E = S$$

Post-multiplication by matrix E defines the operation that relates labyrinth actions to neck actions for any particular muscle.

If we again consider matrix P, but now examine the action associated by pre-multiplication with E we find that this operation relates; (1) excitability changes associated with head and elbow position to that associated for an antagonist muscle of the same limb receiving neck and joint input, and (2) relates the actions on extensor and flexor muscles from opposite limbs receiving the same descending input (labyrinth or neck).

i.e. $E \times P = T$

The above relationships therefore define the operations that exist between labyrinth and neck actions on the excitability of a single muscle, and the relationship between opposite extensor and flexor muscles sharing a common descending input. In addition to these relations, specific relationships also exist between the action of the labyrinth or neck on antagonist muscles in a particular limb and are accessable to a similar treatment.

For example consider the relationship between right extensor and flexor during changes in head and elbow position. In this example, matrix P denotes excitability changes associated with the right extensor and matrix S those observed in the right flexor (see Figs 77a & 78).

In order to map elements in P onto those in S two operations must be performed.

1. matrix P must be pre-multiplied by E

$$E \times P = \begin{pmatrix} 001 \\ 010 \\ 100 \end{pmatrix} \times \begin{pmatrix} XYZ \\ MNO \\ ABC \end{pmatrix}$$

$$= \begin{pmatrix} ABC \\ MNO \\ XYZ \end{pmatrix} = T$$

and 2. matrix T must then be post-multiplied by E, which from above we know will give us S.

$T \times E = S$

Matrix P will then be mapped onto matrix S by the operation

E x P x E = S

this mapping then represents the relationship between antagonist muscles of the same limb receiving head or neck and joint afferent covergence.

In the first step of the transformation defined above the matrix was pre-multiplied by E. This operation yielding in itself one of the other defined matrixes and reveales an operation that relates what is happening in one muscle say the right extensor to what happens to the flexor of the opposite limb.

It would therefore appear that manipulation of a specific matrix by matrix E can provide an idea of what excitability changes occur in other muscles and what changes are associated in the same muscle with a different descending input (labyrinth as opposed to neck or vice versa). In total there are three operations that define the complete spectrum of actions associated with changes in head, neck and elbow position;

1. Pre-multiplication by E relates opposite extensor and flexor muscles sharing the same descending input. This operation reflects the antagonism between the joint mediated actions onto extensors and flexors (i.e. switches row 1 with row 3). Similarly this operation defines the relationship in the same limb to extensor and flexor muscles receiving different descending input (i.e. labyrinth and neck).

2. Post-multiplication by E relates labyrinth and neck actions within a common muscle and in addition relates similar muscles from opposite limbs receiving descending input from the labyrinths or neck (the operation effectively switches column 1 with column 3).

3. Pre-multiplication followed by post-multiplication by E defines an operation in which both rows and columns are interchanged and as such defines relationships extensor and flexor muscles from opposite limbs receiving labyrinth or neck input and also the relationship between flexor and extensor of the same limb when a labyrinth input is switched to a neck input.

The above illustrates the possible relationships found in cats with intact labyrinths. In the following description the situation observed in the left hemilabyrinthectomized cat will be examined.

In the acute hemilabyrinthectomized cat labyrinth reflexes are symmetrical between left and right limbs. As a consequence the operations defining labyrinth and elbow joint afferent interactions are considerably simplified. In the acute hemilabyrinthectomized animal labyrinth and elbow actions can be characterized by just two matrices, one detailing actions to extensors, the other to the flexors. These two matrices can be identified with two of the four described above, namely R and T.

/ZYX\ /CBA\

$$R = \begin{pmatrix} ONM \\ CBA \end{pmatrix} \quad T = \begin{pmatrix} ONM \\ XYZ \end{pmatrix}$$

R - Excitability changes in left and right extensors with changes in head and elbow position.

T - Excitability changes in left and right flexors with changes in head and elbow position.

It is therefore apparent that pre-multiplication with E defines the relationship between labyrinth and elbow actions to extensors and flexors of both right and left sides in hemilabyrinthectomized cats.

$$E \times R = T \quad \& \quad E \times T = R$$

By considering the action of the neck in the hemilabyrinthectomized cat we are again dealing with the basic four matrix conformations.

P - left extensor excitability changes with neck and elbow position.

R - right extensor excitability changes with neck and elbow position.

S - left flexor excitability changes with neck and elbow position.

T - right flexor excitability changes with neck and elbow position.

From this it is clear that neck effects to the right limb parallel the labyrinthine actions to

motoneurones, this defining equallity in effects.

i.e. neck & elbow actions to right flexor
=head & elbow actions to right flexor

This situation equating to the matrices being multiplied by the identity matrix I.

$$I = \begin{pmatrix} 100 \\ 010 \\ 001 \end{pmatrix}$$

e.g. in the case of left hemilabyrinthectomy the labyrinth actions to the right limb are in the same sense as the neck actions.

$I \times T = T$

$I \times R = R$

In relating neck actions to labyrinth actions in the left limb the situation defined for the normal cat also is true for the acute left hemilabyrinthectomized cats.

The operations defined in this appendix, that is pre and post multiplication with matrix E summarize the reciprocal relations that exist between the labyrinth and neck descending actions and the reciprocal actions to extensor and flexor motoneurones mediated by articular mechano-receptors.

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